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United States National Museum
Bulletin 208

THE HONEY-GUIDES

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United States National Museum

1955

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The scientific publications of the National Museum include two series known, respectively, as *Proceedings* and *Bulletin.*

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The present work forms No. 208 of the *Bulletin* series.

Remington Kellogg,
Director, United States National Museum.

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Acknowledgments

In the course of most extensive studies many hands contribute to the end result, but in few have so many kind and able collaborators assisted as in this one. My personal field work in southern and eastern Africa was supported, first, in 1924–25, by the National Research Council with funds supplied by the Rockefeller Foundation, and later, in 1950–51, by grants from the John Simon Guggenheim Memorial Foundation, the American Philosophical Society, and the Smithsonian Institution. Without these sponsoring organizations the work would not have been possible, and in acknowledging their basic aid I can only hope that the results here brought together may justify their confidence and their support.

During the work in Africa practically everyone approached was cooperative and helpful, and the number of individuals who contributed information, advice, or direct assistance in the actual field work is too large to list here. However, the following deserve special grateful mention: E. H. Ashton, R. I. G. Attwell, K. de P. Beaton, C. F. Belcher, C. W. Benson, H. A. W. Bladen, G. J. Broekhuysen, W. Büttiker, E. L. Button, W. L. Chiazzari, T. M. Crooks, W. K. Culbert, E. Davison, E. H. Edwards, R. Guy, H. H. Hamling, E. L. Haydock, J. Hewitt, R. A. F. Hurt, C. H. Jerome, H. M. Miles, B. V. Neuby-Varty, M. E. W. North, G. H. Patten, C. R. S. Pitman, D. C. H. Plowes, H. B. Potter, C. D. Priest, V. L. Pringle, G. A. Ranger, the late A. Roberts, Miss C. Robinson, P. Rougeot, J. Sabater, C. J. Skead, R. E. Symons, J. S. Taylor, R. C. Tredgold, F. G. Turberville, V. G. L. van Someren, A. W. Vincent, J. Vincent, C. M. N. White, C. Whybrow, and J. G. Williams. Some of these individuals I did not have the opportunity to meet, but they aided me by sending painstaking descriptions of observations they had made, others told me at length of such matters, and still others helped with actual facilities for work in the field, or put me in their debt for hospitality graciously extended.

Gordon A. Ranger and C. J. Skead deserve particular mention, as their contributions to the work were of unusual magnitude and quality. Ranger introduced me to the scaly-throated honey-guide near Kei Road, and all my observations on this species were made in his company and with the benefit of his experience and efforts. He and Skead gave nearly two weeks of their time in camp with me, and the information gathered there on three species of honey-guides (*Indicator indicator*, *I. minor*, and *I. variegatus*) was so important and copious

that it constitutes one of the most valuable additions to previous knowledge of these birds. So cooperatively did we work that it is almost impossible to say which data were due to which observer, and since my departure these two meticulous naturalists have continued to study special phases of the biology of the honey-guides and have most generously sent me their data for inclusion in this report. In the pertinent parts of the text I have attempted to give them credit for their contributions, but no words can adequately express the extent to which I, and all readers of this report, are indebted to them.

In addition to his enthusiastic cooperation in the field, Ranger kindly allowed me the use of a number of his photographs taken after my field work was over, while Skead went to great efforts to make contact for me, by correspondence, a large number of observers in South Africa who might have had some notes of interest. While no one can be more acutely aware than I am of the gaps still present in our knowledge of the honey-guides, I feel confident that, given the time and opportunity, Ranger and Skead will continue to study these birds and will fill, or at least greatly reduce, these lacunae. Their work, done at Umtaleni, has been expedited by the cooperation of the owners of that land, Edgar and Neville Ranger.

Second in scope only to the contributions of Ranger and Skead have been those of Neuby-Varty, Plowes, Potter, van Someren, J. Vincent, and Williams. Their names appear in the text in connection with specific items of interest, but their assistance has permeated a larger part of the general background of this report than these actual mentions would indicate.

I met with similar kind cooperation in my work in the museums. In Paris, J. Berlioz put at my disposal the Gaboon material collected by Rougeot; in London, E. Banks and H. B. Usher helped with facilities for studying the great collections of honey-guides in the British Museum, and Macdonald patiently answered queries about certain specimens. The Congo Museum at Tervuren has loaned important anatomical material through the kind efforts of its former director, Dr. H. Schouteden. In Milan, on an earlier visit in 1936, Moltoni showed me the honey-guides in the collections there. Similar courtesies were given me in the museums of Copenhagen, Genoa, Leiden, Stockholm, Turin, and Vienna. Dr. Stresemann kindly assisted with information on specimens in Berlin, and also brought to my attention an early account of the guiding habit of the greater honey-guide. The honey-guides in the museums of South Africa were made available for study; and for this I am indebted to Dr. Barnard of the South African Museum at Cape Town, Dr. Hewitt of the Albany Museum, Grahamstown, E. C. Chubb formerly of the Durban Museum, P. A. Clancey formerly of the Natal Museum, Pietermaritzburg, Miss Courtenay-

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Latimer of the East London Museum, C. J. Skead of the Kaffrarian Museum, King William's Town, Mrs. T. Campbell of the Transvaal Museum, Pretoria, R. H. N. Smithers of the National Museum of Southern Rhodesia, Bulawayo, and Mrs. Goodall of the Queen Victoria Memorial Museum, Salisbury.

In the United States the authorities of the great museums of New York (J. P. Chapin and D. Amadon), Chicago (A. L. Rand), Cambridge (the late J. L. Peters), Pittsburgh (W. E. C. Todd), Philadelphia (R. M. de Schauensee), and Cleveland (H. C. Oberholser) have generously loaned honey-guide material for study.

In this connection it is only just to make particular mention of the helpful and critical cooperation given by James P. Chapin, our leading expert on African birds. He not only went over much of the material with me but read the entire manuscript of this report, in sections as they were written, and has generously made suggestions and corrections which have improved it greatly. For many years Dr. Chapin has been stimulating people in the Belgian Congo and West Africa generally to study the elusive, mysterious lyre-tailed honey-guide, and has intended to write a special paper on this bird. It is a great pity that pressure of other work has kept him from doing so, as it would have given a better presentation of this species than I have been able to piece together from the published literature. The inclusion of the observations of Rougeot and Sabater, the latter hitherto unpublished, is largely due to Chapin's tireless, stimulating influence.

Mr. T. Harrisson, of the Kuching Museum, has kindly written me of his experiences with the Malayan honey-guide in Borneo, and Dr. Dillon Ripley of Yale University has sent me for study the body of an orange-rumped honey-guide which he collected in Assam.

The problems raised by wax digestion in these birds have led me into the fields of bacteriology and biochemistry where I have had to rely for assistance on several experts who were kind enough to interest themselves in this matter. Dr. W. W. G. Büttiker, formerly of Salisbury, Southern Rhodesia, supplied me with live cultures of intestinal bacteria from *Indicator indicator* that were studied for me by Dr. Joel Warren and Maj. Ray Cowley of the Department of Bacteriology of the U. S. Army Medical Service Graduate School. The chemical analyses of wax from wild bee comb and from the gizzard and various parts of the intestinal tract of two species of honey-guides were made for me by Dr. Albin H. Warth, an eminent industrial chemist interested in waxes and wax technology and chemical director of the Crown Cork and Seal Company in Baltimore, and by Dr. F. P. Veitch, professor of physiological chemistry at the University of

Maryland. These studies are being extended, but it is felt that the information already at hand is sufficient for the purposes of this report.

In my studies of the relationships and phylogeny of the species of honey-guides I have been aided by information about the circulatory system in several species kindly examined by Dr. F. H. Glenny and by data on the jaw musculature furnished by Dr. W. J. Beecher. Dr. Edward A. Chapin has made identifications of insect remains taken from the gizzards of several honey-guides, and Dr. Ira B. Hansen has kindly assisted by preparing material for microscopic examination. At my request Dr. Charles Vaurie kindly made some X-ray photographs of the pygostyle of a spirit specimen of a lyre-tailed honey-guide.

For the colored plates, which enable me to bring to the readers of this report the appearance in life of all the species of honey-guides, thanks are due to the National Geographic Society for four of the five plates; the fifth one was made possible by a special grant from the John Simon Guggenheim Memorial Foundation. A word of appreciation to the artist, Walter A. Weber, for his painstaking and excellent work in these five paintings must likewise be recorded here.

The Honey-guides

Introduction

The honey-guides are a small family of picarian birds related to the barbets, the woodpeckers, and the toucans. The family contains eleven species classified in four genera. All but two of these species are found only in Africa south of the Sahara—the two exceptions are Asiatic in distribution, one in the Himalayas, and one in Burma, Siam, Malaya, Sumatra, and Borneo. These birds, of plain coloration and small size, are of unusual interest to the student of behavior because they are parasitic in their breeding habits and because one section of the family has developed a most remarkable symbiotic relationship with certain mammals—ratels and humans—by "guiding" them to wild bees' nests. It is this habit in the best known species of the family that has given the group its common name, honey-guides, and also its technical one, Indicatoridae. The problems arising from these two aspects of the life histories of these birds could not even be approached intelligently until more factual data were amassed and interpreted, and it was to make this possible that the present study was undertaken and this report written. An example of one of these problems may make this clear.

Prior to this study, the impression one received from the literature was that the honey-guides fed largely, if not wholly, on bee comb and its inclusions (bee larvae, eggs, and honey), but that the birds could not open the wild bees' nests by themselves and therefore had to depend on the aid of ratels and humans, which they "guided" to these potential stores of food. In other words, guiding was thought to be the chief food-getting method used by the birds. To the thoughtful student of animal habits this posed a disturbing problem. Habits, like structures, have their long and involved evolutionary history—a history which can be reconstructed mainly on the evidence for "selective values" in their successive stages. But a habit such as this, whose only apparent use to the bird depends entirely on the cooperation of two wholly separate and independent creatures (bird, and ratel or human) cannot have had any conceivable value until it was perfected by both participants, and perfected in such a way as to be of benefit to the bird. Incipient or intermediate stages in its development would seem to have been quite useless; it was an "all or nothing" situation. It followed that either the literature was misleading and that the picture of the guiding habit was wrongly expressed, or that there was more to it than just the matter of food-getting. Obviously, the only valid approach to the problem was to start at the beginning and to assemble sufficient, reliable, basic descriptive data to enable us to draw a truer picture and to rephrase the questions arising from it.

Similarly, it was impossible to compare the parasitic breeding habits of the honey-guides with those of the cowbirds, cuckoos, and other brood parasites until more information was available. It was essential to make such comparisons, and hence it was necessary to find out more about the honey-guides.

In the pages that follow I have brought together all that is known of these birds from the literature, from museum specimens, from the unprinted observations of many naturalists in Africa, and from my own personal field studies. If at times it may seem that unnecessary detail has been set forth I would remind the reader that our studies are still in the fact-finding stage, and that some of these possibly tedious minutiae may turn out to be revealing and significant in the light of further data on the one hand, and, on the other, may help to qualify or to support some of the statements derived from them and other similar crumbs of evidence. Throughout, every effort has been made to integrate all available knowledge, even when that integration is still on the merely suggestive level. In a field where the gaps in knowledge and in the evidence are so numerous, it seems better to venture occasionally with an interpretation or an opinion not yet wholly provable by the actual data than to follow the safer, but intellectually sterile, course of attempting to understand nothing because it is not yet possible to understand all. In each of these ventures I have tried to point out clearly that the interpretations are tentative, and quite possibly of more temporary than permanent validity. I consider them important and useful because they will serve to direct further inquiries and to arouse more searching questionings. Also, since few of the naturalists resident in Africa and the appropriate parts of Asia have the chance to know the species of the family not found in their own special areas, they are not in a position to apply the data on one or two species to the problems arising from other related forms elsewhere except through the medium of a comprehensive and integrated report.

Biological considerations

Evolution and relationships

The ancestral stock from which the honey-guides (Indicatoridae) evolved was probably more similar, in a general way, to the non-specialized barbets (Capitonidae) than to any other existing birds, but all connections have long since completely disappeared. While the honey-guides do seem to have had a common ancestral bond with the barbets, it does not necessarily imply that they originated in southern Asia as did the barbets, according to the latest student of that group (Ripley, 1945). Thus, while the honey-guides cannot be looked upon definitely as immigrants into Africa from Asia, it does seem probable that the family dates back at least to the time when the forest faunas of Africa and India were much more closely related and connected than they are at present. Although the family is more richly represented in Africa than in Asia and with greater generic as well as specific diversity—which might be thought to imply an African locus of origin and evolution—the two Asiatic species are by no means very closely related to each other. The Malayan *Indicator archipelagicus* is more similar to *I. indicator* of Africa than it is to the Himalayan *I. xanthonotus.* The last-named species, with its very small, stubby bill and its plumage coloration, is actually quite different from the "typical" species of the genus *Indicator* and seems to merit the subgeneric distinction given it under the name *Pseudofringilla* by Hume. This, in turn, suggests considerable antiquity of the group in Asia, making it difficult to infer, from the evidence of present forms and their distribution, whether the family is to be looked upon as originally African or Asiatic.

In his reconstruction of the history of the development and distribution of the African terrestrial vertebrate fauna, Lönnberg (1929) concludes that during the early Tertiary, including the Miocene, Africa had a prevailingly moist climate and was covered by a vast evergreen forest.[1] This forest was inhabited by a fauna largely endemic to it, but containing so many types in common with that of southern Asia as to make a Miocene continuum of the two areas probable. Among the genera common to both regions, Lönnberg mentions *Indicator.* The fact that no honey-guides are known to occur in Madagascar further suggests that the actual spread of the group (whether from Asia to Africa or the other way round) may have taken place during the Pliocene, as at that time Madagascar was completely separated from the African mainland. In fact, Lönnberg reports that Pliocene adjuncts to the African fauna are generally absent from Madagascar, even though they may be widely distributed in Africa and in southern Asia. Lönnberg further concludes that the present forest fauna of Africa consists partly of descendants of the original endemic Miocene fauna and partly of later additions which have become adapted to forest living, and that, similarly, the open bushveld and grasslands of Africa have a fauna that contains a good sprinkling of forms that were originally sylvan in their habitat. It is among these forms that we may consider several honey-guides to belong: *Indicator indicator, I. minor* (except for its western, sylvan race, *conirostris*), *I. variegatus,* and *Prodotiscus regulus.* In this conclusion I am anticipated by Chapin (1932, p. 378), who suggests that the family was perhaps originally a sylvan group, although some of its present species are now found only in the open country. Of the eleven species comprising the family, six are known only in forested areas, three only in more open situations, and two have races in both these types of terrain. The forest dwellers are *Indicator maculatus, I. archipelagicus* (largely?), *I. xanthonotus* (largely?), *Melignomon zenkeri, Melichneutes robustus,* and *Prodotiscus insignis;* the species of the bushveld and grasslands are *Indicator indicator, I. variegatus,* and *Prodotiscus regulus,* while *Indicator minor* and *I. exilis* have races in deep forest and also in bushveld. *Indicator variegatus,* while not a bird of extensive evergreen forests, is somewhat more sylvan than *I. indicator* in many parts of its range. *Prodotiscus insignis,* in its southern race, *zambesiae,* is out of the true forest, and in *Indicator minor* we have a similar ecologically intermediate race, *pallidus,* apparently confined to the broken forest at the edge of the true forest in Nigeria.

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[1] In a paper published after the present manuscript was completed, Moreau (1952) agrees that a continuous pre-Pliocene forest across Africa is a necessary assumption, but considers it doubtful that Africa was suitable for a sylvan condition at that time! As in so much evolutionary reasoning we must always remember the uncertainty of conclusions based on assumptions, however necessary they may seem to be.

While there is fairly general agreement that the honey-guides have their closest affinities with the barbets (Capitonidae), the toucans (Ramphastidae), the puffbirds (Bucconidae), and the woodpeckers (Picidae), it should be admitted that there is some uncertainty as to the degree of closeness they show towards each of these groups. Years ago Garrod, Gadow, and Beddard, among others, considered the Indicatoridae only a subfamily of the Capitonidae. Ridgway (1914, p. 310) kept the two as separate families, but considered them as forming the superfamily Capitones. More recently, Wetmore (1951, p. 20) and Peters (1948, p. 63) have come to a similar conclusion, but they also present an arrangement for the other piciform families, superfamilies, and suborders. They consider the Indicatoridae and the Capitonidae as forming the superfamily Capitonoidea of the suborder Gabulae, which contains two other superfamilies—the Gabuloidea, with the Bucconidae (puff-birds) and the Galbulidae (jacamars), and the Ramphastoidea—containing only the Ramphastidae (toucans)—while the Picidae (woodpeckers) are placed in a separate suborder, Pici. Stresemann (1934, pp. 839–842), on the other hand, considers the two suborders of the order Pici to be the Gabuloidea with the Galbulidae and Bucconidae, and the Picoidea with the Ramphastidae, Indicatoridae, Capitonidae, and Picidae.

Glenny (1944, p. 188) has studied the arteries of the heart region in two species of *Indicator* and informs me (in litt.) that the Indicatoridae have not attained as high a level of arterial arrangement pattern evolution as the Capitonidae but that there is a stronger affinity in this respect between these two families than between the former and the Ramphastidae. He considers the Capitonidae and the Picidae closer to each other than either are to the Indicatoridae. Insofar as one may judge relationships from a mere linear listing, it may be noted that Mayr and Amadon (1951, p. 35) separate the Indicatoridae from the Capitonidae by placing between them the Picidae and the Ramphastidae.

Lowe (1946, p. 110) found that the palatal characters described for *Indicator indicator* by Garrod, and accepted uncritically by Gadow, Beddard, and others, are incorrect and that the condition existing in that species is a bivomerine version of the aegithognathous palate, the so-called saurognathous type of Parker, similar to that found in the woodpeckers. Inasmuch as an investigator is apt to be more directly impressed by his own discoveries than by those of his predecessors, this finding apparently caused Lowe to consider the honey-guides nearer to the woodpeckers than to the barbets. In fact, he admits to considerable hesitation in deciding to give the honey-guides separate status and not to merge the family directly with the woodpeckers. To Lowe's elucidation of the morphological situation I may here add one more point. In the literature it is said by several authors that in the honey-guides the clavicles remain separate, not ankylosing into a furculum, and agreeing in this respect with the barbets and not with the woodpeckers. Stresemann (1934, p. 841) is one of the few writers who state that the clavicles do form a furculum in the honey-guides. My studies, based on skeletons of *I. indicator*, *I. minor*, *I. variegatus*, *I. maculatus*, *I. exilis*, *I. xanthonotus*, *Melichneutes robustus*, and *Prodotiscus regulus*, bear out Stresemann's contention, all of these birds showing a midventral symphysis of the clavicles, as in the woodpeckers, though no hypocleidium is present in any of them.

In his study of the functional anatomy of birds' feet, Steinbacher (1935, pp. 259–260) finds the honey-guides to be more like the barbets than the woodpeckers.

Bearing in mind the differences of opinion, and the additional data just outlined, it seems that the barbets have the greatest number of structural characters in common with the honey-guides, and may therefore be looked upon as being, in all probability, their closest living relatives. It appears that both groups may have descended from a common stock, rather than one from the other. The two families agree in the following characters (in addition to those common to all the groups of piciform birds): Transpalatine process absent; sternum with double notch; manubrium pointed, not bifurcate; oil gland tufted; vinculum present between deep flexor tendons of legs; similar, nonpennaceous structure of barbules at the base of the contour feathers; similar insertion of Tensor patagii brevis; thigh muscle formula AXY; Ambiens muscle absent, the Dermotensor patagii joining the Tensor patagii longus, which, in turn, is joined by a strong slip from the Pectoralis propatagialis; biceps slip absent; Expansor secundariorum absent; only one carotid artery, the left, present; gall bladder long and tubular; the Peroneus brevis with a large tendon of insertion; Peroneus longus absent, cervical haemopophyses single, sharp, channeled; contour feathers with an aftershaft. (List of characters largely compiled from the accounts by Lowe, Gadow, and Ridgway). It should be stated that in slightly more than half these characters the honey-guides, and the barbets, also agree with the woodpeckers. From the barbets the honey-guides differ in the form of the nostrils, which are set in the center of large nasal fossae and surrounded by a broad membrane in the *Indicatoridae*, while in the *Capitonidae* they are bored directly into the horny rhinotheca; the honey-guides are antiopelmous (like the wrynecks and piculets), i. e., the first, second, and fourth toes are connected with the flexor hallucis longus tendon, and the third toe with the flexor digitorum longus; the honey-guides are 9-primaried while the barbets are 10-primaried. In fact, except for the oscine Passeres the family Indicatoridae forms the only 9-primaried group, and, as Miller (1924, p. 315) pointed out, some members of the family are 9-primaried in the strictest sense, as in *Prodotiscus* the tenth (outermost) primary is entirely lacking. In many other honey-guides the tenth small quill is still present, but even smaller than in any of the Oscines. The barbets have 10 rectrices, while the honey-guides (except for the genus *Prodotiscus* which has 10) have 12.

Some of the characters tabulated by Ridgway (1914, p. 310) to differentiate the Indicatoridae and the Capitonidae do not hold to the extent that he thought. The two groups are essentially similar in their pterylosis, the chief difference being that in the barbets (it is not known if this is true of all the genera) there is a noticeable, somewhat diagonal apterium on either side of the chin and throat, whereas the entire chin and throat are feathered in the honey-guides; also, the spinal tract is interrupted posterior to its bufurcation on the back in the barbets while in the honey-guides the two branches come together posteriorly (and these two branches are larger as well). The posterior portion of the spinal tract is narrow and mediodorsal in *Indicator* and there is a short, disconnected supracaudal tract on either side extending anteriorly to about the level of the posterior union of the bifurcations, while in the barbets the posterior end of the spinal tract itself divides to form a circle around the uropygium, leaving the mediodorsal area unfeathered and encompassing the two supracaudal tracts in its course. The apteria generally are somewhat more extensive in the barbets than in the honey-guides. The differences mentioned by Ridgway in the size and shape of the bill and in the relative length of the outer primaries are scarcely characters of familial significance. There is, however, a notable difference in the syrinx, but it must be remembered that our comparison is based on three species of honey-guides (*Indicator indicator*, *I. maculatus*, and *I. exilis*) and a single kind of barbet (*Megalaema asiatica*). In the honey-guides the lower end of the trachea is formed into a solid, osseous box by the fusion of several of the lowermost rings; the first bronchial semiring, to which is attached the single pair of intrinsic muscles, is considerably swollen and much larger than the subsequent ones. In the one barbet examined the syrinx is of a simple tracheobronchial form, the last rings are not fused at all, but are distinct, and there are no intrinsic muscles.

An important character in which the honey-guides agree with the barbets and differ from the woodpeckers is the form of the tongue, which is short and not extensible or protrusible.

The phylogeny of the species of honey-guides within the family now seems fairly clear, although in the past literature it seemed otherwise, as may be sensed from the disparity in the treatment presented between even two linear lists such as those of Sharpe's hand-list of 1900 and Peters' of 1948. Sharpe lists the genera in the following order: *Indicator*, *Prodotiscus*, *Melignomon*, while Peters gives *Prodotiscus*, *Melignomon*, *Indicator*, *Melichneutes*. For such a small avian family, containing only 11 species, the Indicatoridae has numerous and divergent subdivisions—4 genera, of which 2 (*Melichneutes* and *Melignomon*) are monotypic and 1 (*Prodotiscus*) has only 2 species, while the only genus with several members (*Indicator*, with 7 species) is readily divisible into 3 subgenera (4 species in subgenus *Indicator*, 2 in *Melignothes*, and 1 in *Pseudofringilla*). It seems that the process of differentiation was probably completed (at the present level) long enough ago to allow for the subsequent disappearance of intermediate stages, and also that the main lines of differentiation came not so much in chronological sequence from earlier derivatives from the original stock but directly from the original stock itself. As far as may be judged from the structure and external character of the present species, there were three radiating branches from the original ancestral stock. Bearing in mind the probable similarity of the primitive honey-guides to the nonspecialized barbets, it seems that this original stock was generally more similar to the large-billed species of *Indicator* (subgenus *Indicator*) than to any of the other present forms. Adding to this the likelihood of the family being originally a forest-dwelling group, it would seem that *Indicator maculatus* of the West African forests is as near as any to this ancestral group. The development of *I. maculatus* is thus the base of the first line of descent, and from it, or from something akin to it, developed two branches, one leading through *I. variegatus* to *I. archipelagicus* and *I. indicator* and the other leading from *I. variegatus* to *Melichneutes robustus*. It may be noted that it is only in that branch of the phylogenetic tree of the group that leads from *I. variegatus* to *I. indicator* that we find evidence of the guiding habit. Whether this remarkable habit is also exhibited in *I. archipelagicus* is, unfortunately, unknown, and further information on that species is apt to be very slow in coming in. That *I. variegatus* is less advanced than *I. indicator* is in agreement with the slight development of guiding in the former as compared with its great development in the latter. The intermediate position of *I. variegatus* between *I. maculatus* on the one hand and *I. archipelagicus* and *I. indicator* on the other is further suggested both by its coloration (losing the heavily maculated pattern of its "ancestor" and approaching the plainer pattern of its "descendants") and by its voice (its purring note being apparently reflected in the catlike *mia-ow krruuuu* of *I. archipelagicus*).

A second line of differentiation—expressed chiefly in the reduction in the size of the whole organism, particularly the length of the bill—may be traced from the hypothetical ancestral stock to that which bifurcated into the subgenera *Melignothes* and *Pseudofringilla*. The former of these produced *I. minor* and its races, and then, by further reduction in over-all size, *I. exilis* and its subspecies; the latter is evident only from its one known end product, *I. xanthonotus*.

The third line of descent, involving originally chiefly the narrowing of the bill, produced *Melignomon zenkeri*, and then, through the loss of one pair of rectrices and the development of a softer, fluffier plumage, *Prodotiscus insignis,* and finally, on emerging from the forest into the bushveld, *Prodotiscus regulus.* The genus *Prodotiscus* is the most divergent from typical *Indicator* of all the honey-guides, and it is less closely alied to *Melignomon* than the above brief statement may suggest. It seems, however, that *Melignomon zenkeri* does represent a first stage on the path that led from *Indicator* to *Prodotiscus,* but it is very much nearer to the former than to the latter genus; in fact, *Melignomon* could readily be called only a subgenus of *Indicator.* That *Prodotiscus regulus* is a further development than *P. insignis* is suggested by the fact that in its immature plumage it has the outer rectrices similar in pattern to those of *P. insignis* (adult and young), and also by the fact that it is a denizen of more open country, not of the true forests.

The apparent phylogenetic relationships of the species of honey-guides are expressed in the accompanying diagram (fig. 1). Their classification into genera, species, and races follows that given in my recent systematic revision of the group (Friedmann, 1954b).

No one character has had a more varied history in the phylogeny of the honey-guides and their relatives than has the form of the tail. Starting from a presumably 12-rectriced group, these birds retained this number while the barbets became 10-rectriced, and it is only in the most divergent of their genera, *Prodotiscus,* that the honey-guides have lost one pair of rectrices. Also, the genus *Indicator* gave rise, through the remarkable alteration of an originally plain, unspecialized tail, to the highly peculiar form of the lyre-tailed species, *Melichneutes robustus.* Furthermore, in at least two species of *Indicator* (*indicator* and *minor*) a rustling flight, possibly involving the tail feathers, is known to take place. In the not distantly related woodpeckers, the tail feathers went through very striking functional modifications as well.

While not contributing significantly to our understanding of the relationships of the various species of honey-guides, the following anatomical notes, based on an examination of 8 of the 11 species and all additional to the previously published data, seem worthy of record here. Fürbringer's (1888) extensive observations on the myology of *Indicator indicator* are not discussed because I have no similar data on the other species with which to compare them. There would seem to be little likelihood of any essential differences in their musculature, however.

The sternum shows remarkable variation in the development of the keel. In some species of the genus *Indicator* (subgenera *Indicator* and *Melignothes*) the keel is fairly well developed, about as in a number of barbet genera examined; in *Indicator xanthonotus* (subgenus *Pseudofringilla*) and in *Melichneutes robustus* it is noticeably shallower at its anterior end and almost disappears posteriorly. While I have examined only a single example of each of these two, my observations on *Indicator xanthonotus* bear out exactly what Stoliczka (1873, p. 426) described many years ago for another specimen, writing that the "keel is moderately elevated in front, but after a short distance rapidly diminishes in height, and becomes almost obsolete before it reaches the end of the sternum." Bates (1909b, p. 27) commented on the remarkably depressed body form of *Melichneutes*, and noted that the sternal keel was shallow; I find it is less well developed in that species than in any of the other members of the family examined. The aberrant genus *Prodotiscus*, on the contrary, has a remarkably deep keel. In order to clarify the great differences

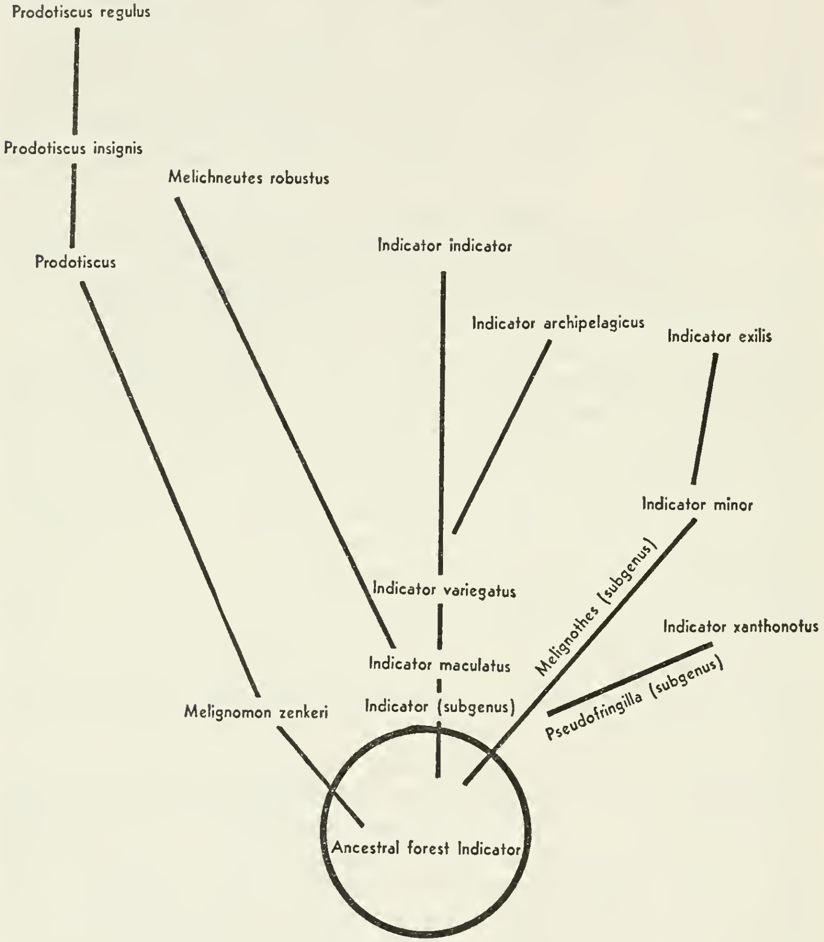
Prodotiscus regulus
Prodotiscus insignis
Melichneutes robustus
Prodotiscus
Indicator indicator
Indicator archipelagicus
Indicator exilis
Indicator minor
Melignothes (subgenus)
Indicator variegatus
Indicator xanthonotus
Pseudofringilla (subgenus)
Indicator maculatus
Melignomon zenkeri
Indicator (subgenus)
Ancestral forest Indicator

Figure 1.—Phylogenetic tree of the honey-guides.

in this character, the accompanying illustration (fig. 2) shows the sterna of the eight species examined drawn as if they were the same size. To keep these diagrams as simple as possible the processus lateralis anterior has been left out in all cases. If we take the greatest height (perpendicular) of the keel, and the total length of its base to the tip of the manubrium, the former varies from 23 to 29 percent of the latter in the species of *Indicator* and *Melichneutes*, while in *Prodotiscus* it is 43 percent of the basal length. The degree of development of the sternal keel does not appear to be correlated with observable differences in flight as far as the honey-guides are concerned. Certainly *Prodotiscus* does not give the impression of being a stronger or more rapid flyer than *Indicator*, while the remarkable aerial evolutions of *Melichneutes* are produced by the species with the least developed keel of all the members of the family. Parenthetically, it may be remarked that when Sclater (1870, p. 178) described the processus lateralis posterior and the processus intermedius as being

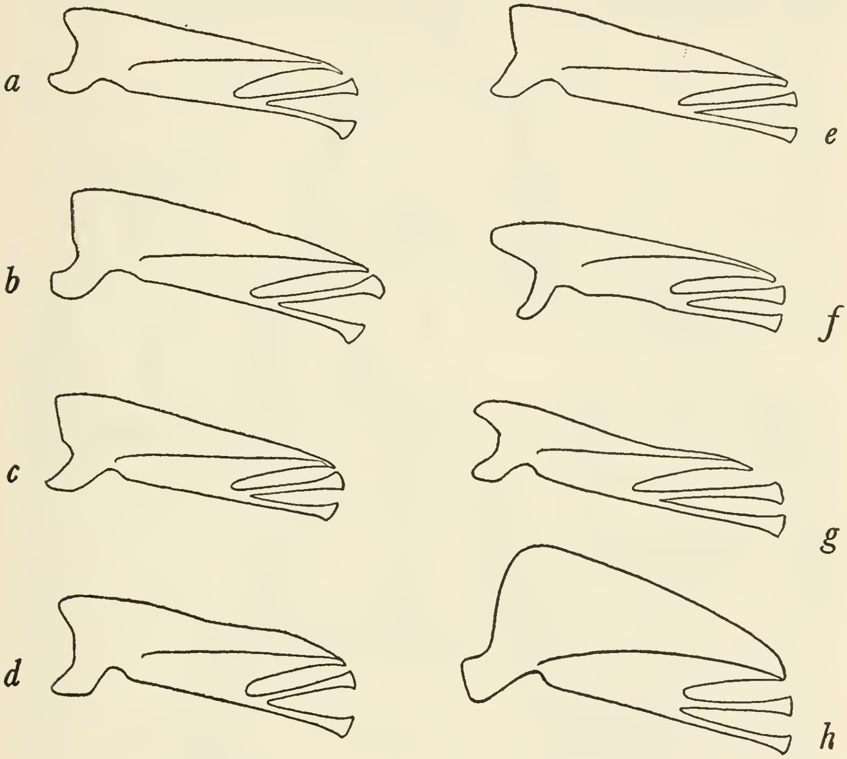

FIGURE 2.—The sternum in eight species of honey-guides, all drawn to same size: *a*, *Indicator maculatus;* *b*, *Indicator variegatus;* *c*, *Indicator indicator;* *d*, *Indicator minor;* *e*, *Indicator exilis;* *f*, *Indicator xanthonotus;* *g*, *Melichneutes robustus;* *h*, *Prodotiscus regulus.*

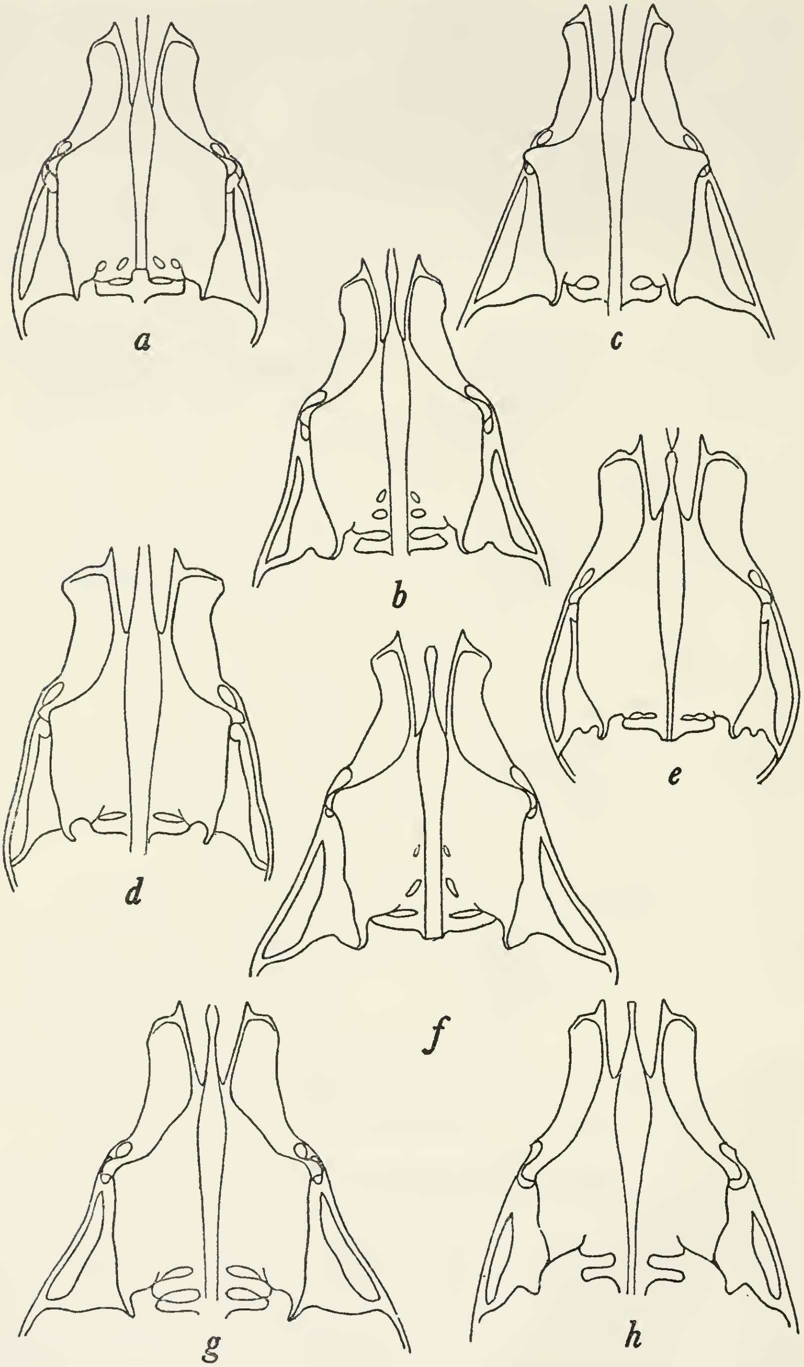

Figure 3.—For explanation see opposite page.

united distally he apparently had an imperfectly cleaned skeleton before him. As may be seen from our illustration, these two processes are free terminally. The sternal notches (between the processus lateralis posterior and the processus intermedius and the metasternum) are relatively somewhat deeper in *Prodotiscus* and *Melichneutes*, and shallower in *Indicator* (especially so in *I. indicator* and *I. minor*).

The synsacrum varies less strikingly, but also reveals a few minor characters of interest. Here it is essential to compare only specimens of the same sex (see fig. 3). Again *Prodotiscus* deviates the most from the main stem of the family; in it the acetabular process is relatively much farther back, making the anterolateral margin of the area dorsalis of the pars renalis of the ischium more steeply diagonal, the linea iliolateralis relatively shorter, and the pars glutea of the ilium longer and narrower than in the species of *Indicator* and *Melichneutes*. The ilium is slightly longer, relatively, in *Melichneutes* than in *Indicator indicator*. The pars glutea of the ilium is considerably broader in *Indicator xanthonotus* than in any of the other species examined, as may be seen from the diagrams; the anterior portion of its synsacrum being thereby made almost as broad as the area dorsalis of the ischium. The nearest approach to this characteristic is found in *Indicator maculatus*.

The coracoids of *Melichneutes robustus* have the sternocoracoidal process much blunter than in *Indicator variegatus* (in which species they are curved and pointed anterolaterally), agreeing in this respect with *I. indicator*, *I. exilis*, and *I. minor*.

The clavicles are ankylosed medioventrally in all the honey-guides, forming a true furculum, but always lacking a hypocleidium.

The description by Lowe (1946, p. 106) of the skull of *I. indicator* is fully borne out by my own study of this species. The skull of *I. variegatus* is similar, with the following slight differences: Anterior ends of the vomers touch the prepalatines (considerable space between them in *I. indicator*); the posterior ends of the palatines are thinner and the transition from this thinness to the broad flaring portion is more abrupt and sudden; the maxillopalatines appear to meet in the midline dorsal to the vomers; the pterygoids are more dilated anteriorly; the basioccipitals are somewhat convex ventrally and are divided by a median groove (not indicated in Lowe's figure of *I. indicator*); the whole skull is slightly broader posteriorly. In *Indicator exilis* the vomers are bowed laterally more than in either *I. indicator* or *I.*

FIGURE 3.—The synsacrum in eight species of honey-guides, all drawn to same size: *a*, *Indicator variegatus*, ♂; *b*, *Indicator indicator*, ♂; *c*, *Indicator exilis*, ♂; *d*, *Indicator xanthonotus*, ♂; *e*, *Indicator maculatus*, ♀; *f*, *Indicator minor*, ♀; *g*, *Melichneutes robustus*, ♀; *h*, *Prodotiscus regulus*, ♀.

variegatus; the interpalatine spurs are relatively longer than in *I. variegatus*, agreeing in this respect with *I. indicator;* the pterygoids are slightly more slender, less widened anteriorly than in *I. variegatus.* The skull of *I. maculatus* agrees in all respects with that of *I. variegatus.*

The gizzard is thin-walled, quite remarkably so in *I. minor, I. indicator, I. xanthonotus, I. variegatus, I. maculatus* and *I. exilis;* in *Melichneutes robustus* it is slightly more muscular, i. e., thicker, and in *Prodotiscus regulus* it is thicker than either. My observations are anticipated by similar findings on *I. minor* by Sclater (1870, p. 178) and Blanford (1870, p. 308).

Tongues of *Melichneutes robustus, Indicator maculatus, I. minor, I. variegatus,* and *I. exilis* were examined. They are all similar to the tongues of several barbet genera with which they were compared, and show no special adaptation towards cerophagy. The tongue of *Melichneutes* is slightly narrower and longer than that of *Indicator maculatus* and has a slight basal restriction not noticeable in the latter.

After studying the various families of piciform birds Beecher (1953, p. 298) concludes that the "jaw muscle pattern shows a strong facies resemblance in all . . . . The honey-guides have the least specialized pattern and may represent the ground plan from which the other families have been derived, though other indications are that the barbets are nearer the ancestral stock . . . . Bills and feeding habits suggest close but disjunct relationships in a single series and plumage suggests origin of piciform families from the barbets or an ancestral group with a somewhat less pronounced bill."

Phylogeny of brood parasitism

The parasitic mode of reproduction is known definitely in *Indicator indicator, I. minor, I. variegatus, I. exilis,* and *Prodotiscus insignis.* There is suggestive evidence for it in *Melichneutes robustus* and *Prodotiscus regulus.* Nothing is known of the breeding of *Melignomon zenkeri,* the two Asiatic species of *Indicator,* or *I. maculatus* of West Africa. The last named is very closely related to *I. variegatus,* almost closely enough to be considered conspecific, and it would be surprising if it were other than similarly parasitic. Also, *Melignomon* forms a link between *Indicator* and *Prodotiscus,* having the 12 rectrices of the former and the thin bill of the latter; in other words, it is a genus intermediate between two parasitic genera, and is therefore probably not different in its breeding habits. It seems safe to say that the parasitic habit is older in the family Indicatoridae than is the evolution of the group into its present generic sections, the two most divergent portions of the family, *Indicator* and *Prodotiscus,* being parasitic. Indeed, it appears that the parasitic habit is probably older in the honey-guides in relation to their total history as a family of birds than it is in any of the other four avian families exhibiting this mode of reproduction. In the Icteridae and the Anatidae parasitic breeding is a relatively recent development, as it also seems to be in the Ploceidae (where it has actually developed twice in unrelated parts of the family). In the Cuculidae it gives evidence of greater antiquity (it is distributed over a larger number of genera and species, and possesses, in some cases, extreme specializations of host specificity, of host egg resemblance, and of eviction of nest mates by the nestling parasite). In the Indicatoridae alone do we find that the majority (possibly all) of the included species are parasitic. Also, in this family we find that the birds have "lost" more of the "ordinary" features of the reproductive behavior cycle than in the other parasitic groups. To use the terminology of Kendeigh (1952), the honey-guides show less "attentive behavior" than do the other parasitic birds. The general scarcity of courtship and the lack of any signs of mutual exclusiveness between males (of *I. indicator* and *I. minor*, at least) at the stud posts (see p. 125) are significant. The difference between the highly developed and much-indulged-in courtship behavior in the parasitic cowbirds and weavers, and even some cuckoos, and the lack or infrequency of such behavior in the honey-guides is striking. On the other hand, it is true that a type of rustling flight, reaching a remarkable degree of evolution in the lyre-tailed species, has developed in these birds, but whether it is really a form of mutual courtship activity is not yet clear.

Together with this phylogenetic "loss" of parts of the behavior cycle, there are a number of "gains" or developments that have transpired in connection with the parasitic habit in the Indicatoridae. The most striking of these is the development of a pair of bill hooks in the newly hatched chicks of at least two and possibly other species of the genus *Indicator*. Just how many species of honey-guides have these hooks is not known, but it is now clearly understood that they are used in the process of eliminating nest-mate competition by the young bird. It is true that as yet we have direct observations on but single instances of nest-mate attack or eviction by two species of honey-guides (*I. indicator* and *I. minor*), and in one of these species (*I. indicator*) the adult female often does away with the need for such attack by puncturing the eggs when laying its own in the nest. In this matter of getting rid of nest mates the parasitic habit in the honey-guides agrees with that in some of the cuckoos, but not with that in the weavers or in the black-headed duck (the only parasitic duck). Cowbirds frequently eliminate nest mates by severe competition with them for food by the young parasite, and not by direct attack on them.

Knowledge of the breeding of too many of the honey-guides is still insufficient to permit of generalizations of more than temporary usefulness. It may be mentioned, however, that egg-pecking by the laying hen is much more frequent in *Indicator indicator* than in *I. minor;* that in the majority of cases for both these species only one egg is deposited in any one nest; that in the majority of cases the young parasite is the sole survivor of the nest contents. The species of *Indicator,* as far as known, largely restrict their parasitism to hole-nesting birds (including species that breed in enclosed nests, such as some swallows). While the ornithologist may consider it "only natural" for a picarian bird such as *Indicator* to lay its eggs in nests of a picarian type, it must be emphasized that the birds involved are by no means all of this sort. Starlings of several species, ant-eating chats, swallows, and yellow-throated sparrows are victimized as well as barbets, woodpeckers, bee-eaters, and hoopoes. Furthermore, *Prodotiscus insignis* departs even further, laying its eggs in open cup-shaped nests of species of *Zosterops* and *Apalis,* a completely dissimilar group of hosts. We know almost nothing of the nestling stage of *Prodotiscus,* but in *Indicator* the range of hosts poses a very interesting problem. As Lack (1948, p. 33) has shown, birds with short incubation periods have short nestling periods as well (by nestling period is meant the time from the hatching of the egg to the time when the young bird is ready to leave the nest), but there is one notable exception to this rule—the barbets, woodpeckers, toucans, and their relatives, in which the incubation period is fairly short (a little over two weeks) while the nestling period may be a month or even longer. The honey-guides (at least *Indicator*) agree with this group, having incubation periods of about 12–16 days, and nestling stages of from 35–40 days. This means that a honey-guide in a barbet's, woodpecker's, or hoopoe's nest fits fairly well into the normal time limits of the host's breeding cycle, but that one in the nest of a sparrow, swallow, chat, or starling greatly prolongs the normal duration of nestling care and feeding for the foster parent. And yet these birds can and do rear honey-guides. One may only wonder if the group of activities loosely covered by the term "care of nestlings" is one of those things that grows on itself and is therefore capable of very considerable extension. It would seem, however, that probably the range of host species was originally more restricted to birds of similar breeding cycle characteristics when the parasitic habit began in the honey-guides than it has since come to be. Even now, the passerine host records are considerably fewer in number than are those of picarian and coraciiform victims. This further suggests that the host predilections of *Prodotiscus insignis* are relatively recent, which is in keeping with the conclusion that *Prodotiscus* evolved, through a *Melignomon*-like stage, from an *Indicator*-like ancestral stock. The duration of the nestling stage in *Prodotiscus* is one of the many facts sorely needed to round out a study of the honey-guides. It would be highly interesting to know if this tendency to parasitize small passerines such as white-eyes and bush warblers is accompanied by an accelerated nestling growth rate.

The fact that in their ontogeny the species of *Indicator* are birds of slow development forms a point of striking difference from all other groups of parasitic birds—cuckoos, cowbirds, etc. In the literature it is often assumed that rapid nestling growth has a definite selective value for a parasite having to compete with a variety of nest mates. The honey-guides show that this is not always true.

The eggs of all the honey-guides yet known (and probably those still to be described) are plain, unmarked white, like those of barbets, woodpeckers, and other picarian birds. Inasmuch as the majority of the host species (except for those of *Prodotiscus insignis*) are also of picarian or coraciiform affinities and lay unmarked, whitish eggs, it follows that in all these cases there is a close agreement in coloration between the eggs of the parasite and of the victim. That such agreement is not essential, however, is indicated by the fact that the honey-guides have equal success with starlings, swallows, chats, woodhoopoes, and other birds whose eggs are quite dissimilar to those of the parasite. It is possible that the darkness prevailing in the nesting holes of these hosts may reduce the possible selective value of egg resemblance.

Another point of departure from what we find in many other parasitic birds is that the known eggs of the honey-guides are not generally larger than those of their common hosts; in fact they are frequently considerably smaller. Thus, the black-collared barbet, *Lybius torquatus*, the most frequent victim of the lesser honey-guide, *I. minor*, lays eggs that measure 23–25.5 by 17–18.5 mm. as against 20.3–22.6 by 14–17.5 mm. for those of the parasite. The eggs of the honey-guides are not small for the size of the bird, as in some cuckoos of the genus *Cuculus*. They do not appear to have shorter incubation periods than those of the common host species, but on this point reliable data are very scanty.

Inasmuch as all the honey-guides of whose breeding habits we have any knowledge are parasitic, they afford little in the way of clues as to the mode of origin of this habit. Similarly the data, admittedly poor, on the various species of barbets, their supposedly closest relatives, give no hint as to any incipient trends towards parasitic reproduction. The barbets (or, more correctly, a few species of barbets that have been studied) are birds in which both sexes take part in excavating the nesting hole, and share alike the tasks of incubating the eggs and of feeding and caring for the young.[2] In other words, the stock closest to the honey-guides are birds in which both sexes are active in all phases of the normal sequence of reproductive activities, and this, in turn, suggests that the originating factor or factors that led to parasitism in the Indicatoridae were probably such as affected both sexes more or less equally.

The fact that some of the barbets have the habit of using old nest holes of other species as well as their own for sleeping places during the nonbreeding season, and that they often are quite gregarious in these "dormitories," vaguely suggests the possibility that the mutual exclusiveness of nesting sites normal to most birds (and to barbets also) may be subjected to some infringement or weakening thereby.[3] However, this is only a passing thought; it may help to account for the tendency of *Indicator minor* to enter nest holes of barbets and other birds even when not in breeding condition itself. So far, nothing is known of the sleeping habits of honey-guides, whether they use old excavations in trees as dormitories or whether they pass the night amid the dense foliage of the trees. Any information on any usage by honey-guides of old nesting sites of other birds may well provide suggestive data.

Although nothing is known as to the factors that may have conditioned, if not brought about, the advent of brood parasitism in the honey-guides, we have some slight evidence as to the geological time of their operation. In our discussion of the evolution of the species of honey-guides it was pointed out that the family is of at least Miocene age, and that its geographic spread appears to have taken place in the Pliocene. The fact that the parasitic habit is present in all sections of the family suggests that it is of greater antiquity than the differentiation of the group into its component species and genera, and this, in turn, suggests that the original honey-guide stock probably was parasitic prior to the Pliocene spread of the family. In his recent study of the evolution of parental care in birds, Kendeigh (1952, p. 297, footnote) writes that the evolution of the different behavior patterns of the various families and orders of birds probably developed chiefly during the sixty million years of the Cenozoic period. The fact that a reproductive mode such as brood parasitism could hardly have become successful until the patterns of parental care in the various hosts were well fixed further indicates that these patterns were not more recent than the Miocene, and probably older. This fits in very well with Kendeigh's general statement.

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[2] This is also true of the related puffbirds (*Bucconidae*), in three species of which both sexes are known to share these duties. (Skutch, 1948.)

[3] Thus, in the Central American prong-billed barbet, *Semnornis frantzii*, Skutch (1944) found as many as 16 birds in one such dormitory, although as the breeding season approached the paired barbets began to sleep in their own nests and these dormitories became deserted.

Brood hosts

The following generalizations must be read with the mental reservation that we still know nothing of the brood hosts of five of the eleven species of honey-guides, and very little of those of three of the remaining six. Of these six, the data are relatively extensive for only two, the greater and the lesser honey-guides, but inasmuch as these two occur in the same habitat in many parts of Africa, it is possible to see what, if any, differences they reveal in their choice of hosts. The two together are known to parasitize some 39 species of birds (not counting subspecies), and 12 of these 39 serve as brood hosts to both. Of the 27 other species, a little more than half are birds with single, or at most two, host records each, but some of the rest appear to reflect definite differences in the range of selective parasitism preferences of the two honey-guides. Nests in holes in the ground are utilized relatively seldom by *I. minor* (3 instances out of 50+ host nest records), but are frequently parasitized by *I. indicator* (44 cases out of a total of 96 host nest records). Bee-eaters, hoopoes, kingfishers, and pied starlings are the chief ground-tunnel nesters victimized by *I. indicator*, and these birds are obviously far more important to the greater than to the lesser honey-guide. While it is true that barbets and woodpeckers are relatively more favored by *I. minor* than by *I. indicator*, the latter uses these hosts often enough to make it clear that they are satisfactory for its purposes as well. Thus, in my files are 19 records involving 5 species of barbets and 4 of woodpeckers for *I. indicator* and over 40 records involving 9 species of barbets and 6 of woodpeckers for *I. minor*. To put it somewhat differently, approximately 20 percent of the host records for *I. indicator* (actually 19 out of 96) are for barbets and woodpeckers, while for *I. minor* this figure is 80 percent (over 40 out of 50+ records).

The known choice of victims of *I. variegatus* and *I. minor* shows a remarkable degree of sameness throughout. The data at present available for the variegated honey-guide involve 11 species of hosts. Of these, all but one are also parasitized by the lesser honey-guide (and that one leaves something to be desired as to the identification of the parasite).

One host species in southern Africa, the yellow-throated sparrow, *Petronia superciliaris*, is parasitized by two kinds of honey-guides found there (*I. indicator*, *I. minor*) and has been suggested as a host of a third (*P. regulus*) and even of a fourth (*I. variegatus*). Another host species in tropical Africa, the golden-rumped tinkerbird, *Pogoniulus bilineatus*, is recorded as a victim of four species of *Indicator*

(*indicator*, *minor*, *variegatus*, and *exilis*), but there is some doubt as to the identification of some of the parasites involved. Barbets and woodpeckers offer the greatest number of multiple parasite host species, two species of each (*Lybius torquatus*, *Trachyphonus vaillantii*, *Campethera nubica*, and *Campethera abingoni*) being recorded as victims of each of three species of honey-guides, while three other barbets (*Stactolaema anchietae*, *Pogoniulus pusillus*, and *Tricholaema leucomelan*) and one other woodpecker (*Dendropicos fuscescens*) are known to be parasitized by two species of honey-guides.

Aside from the genus *Prodotiscus*, as yet known to parasitize only small passerine birds, it seems that the "typical" honey-guides (genus *Indicator*, and probably *Melichneutes*) victimize picarian and coraciiform birds primarily, and only such passerine forms as utilize old nesting sites of these birds or other tunnels fairly similar to theirs. It may be pointed out that the other parasitic birds of Africa (cuckoos and weavers), with the exception of the great spotted cuckoo, *Clamator glandarius*, rarely affect hole-nesting species; consequently, there is little if any conflict or competition for brood hosts between them and the typical honey-guides. Two species of starlings (*Spreo bicolor* and *Lamprocolius nitens*) are the only hosts known to be parasitized frequently by both a cuckoo (*Clamator glandarius*) and a honey-guide (*Indicator indicator*). In no one nest have eggs of both of these parasites been found together.

Mandibular hooks of nestlings

The presence of needle-sharp, semitransparent hooks on the tips of the maxilla and mandible of nestling *Indicator indicator* and *Indicator minor*, and probably of other species of the genus, seems to be a remarkable specialization that is of adaptive significance to the nest life of a parasitic bird. These structures are definitely known only from two species, *I. indicator* and *I. minor*, and from an unfeathered chick attributed to *I. variegatus* on inconclusive evidence. Haagner and Ivy (1907a, p. 4) write that while the "hooks apparently fall off when the bird is fully adult . . . there are traces of their existence in the slightly flattened end of the premaxilla, and the membranous scaly appearance of the terminal portion of the mandible of several adult specimens of *Indicator sparrmani* [=*I. indicator*] and *I. minor* examined by us. The beaks of the adult specimens of *Indicator* have the culmen and genys much more curved than that of the young bird under discussion, and it is therefore easy to see where the hooks part from the beak, and by the distinctly welded appearance of the whole structure they are very obviously only superficially connected."

Inasmuch as these hooks are temporary structures that are shed considerably before the young bird is ready to leave the nest, it follows that in cases where observers have stated that nestlings did not have any bill hooks it does not necessarily mean they never had any. Even in *Indicator indicator* and *I. minor*, where we have ample evidence of these bill hooks, there are cases where observers saw no sign of them on nestling birds. Apparently the nestlings were found after they had shed the bill hooks. Bearing in mind that the absence of hooks in a half-grown chick is no proof that the bird may not have had them, it may be noted that such a hookless condition has been reported for *Melichneutes robustus* (one specimen), and for the West African forest race of the lesser honey-guide, *I. minor conirostris*. It is doubtful that a character of this sort would be present in one race and absent in another of the lesser honey-guide, and it seems probable that hooks are present in all the honey-guides, except possibly *Prodotiscus*.

In order to ascertain the structural nature of these hooks, the bill of a two-day-old *Indicator indicator*, collected by Mr. Graham H. Patten, was serially sectioned, stained, and studied microscopically. As the photomicrograph of a sagittal section of the maxilla (pl. 1, top) shows clearly, the hook is merely a continuation of the egg-tooth material distally over the end of the maxilla and prolonged into a decurved point. The mandibular hook showed the same type of structure, but unfortunately it broke off from the mandible while being sectioned and therefore the resulting slides, while anatomically informative, do not lend themselves to illustrative purposes.

With the photomicrograph of the honey-guide maxillary hook are shown copies of some of Gardiner's (1884) drawings of bill formation in an embryo of the domestic chick (fig. 4,*d–f*). When the bill first develops the two jaws are originally one closed continuum, and the egg-tooth is formed on the dorsal surface before the two are separated by the invagination of the oral groove from the tip of the bill. In the figure showing the early stages of this invagination (fig. 4,*d,f*) the future mandible is turned up at the tip and the path of the invagination also causes an original downward deflection of the tip of the future premaxilla. If these terminal curvatures were somewhat elongated and retained we would get what we find in the honey-guides, where they form the bill hooks. Furthermore, in the cross-section of the bill of an embryo kite (*Milvus milvus*) (fig. 4,*g*), Gardiner found a terminal papillum, which, if it were recurved instead of decurved, would be essentially the same as the mandibular hook of a honey-guide.

While no one hitherto had made a histological study of these hooks, they were generally assumed to be direct derivatives from the egg-

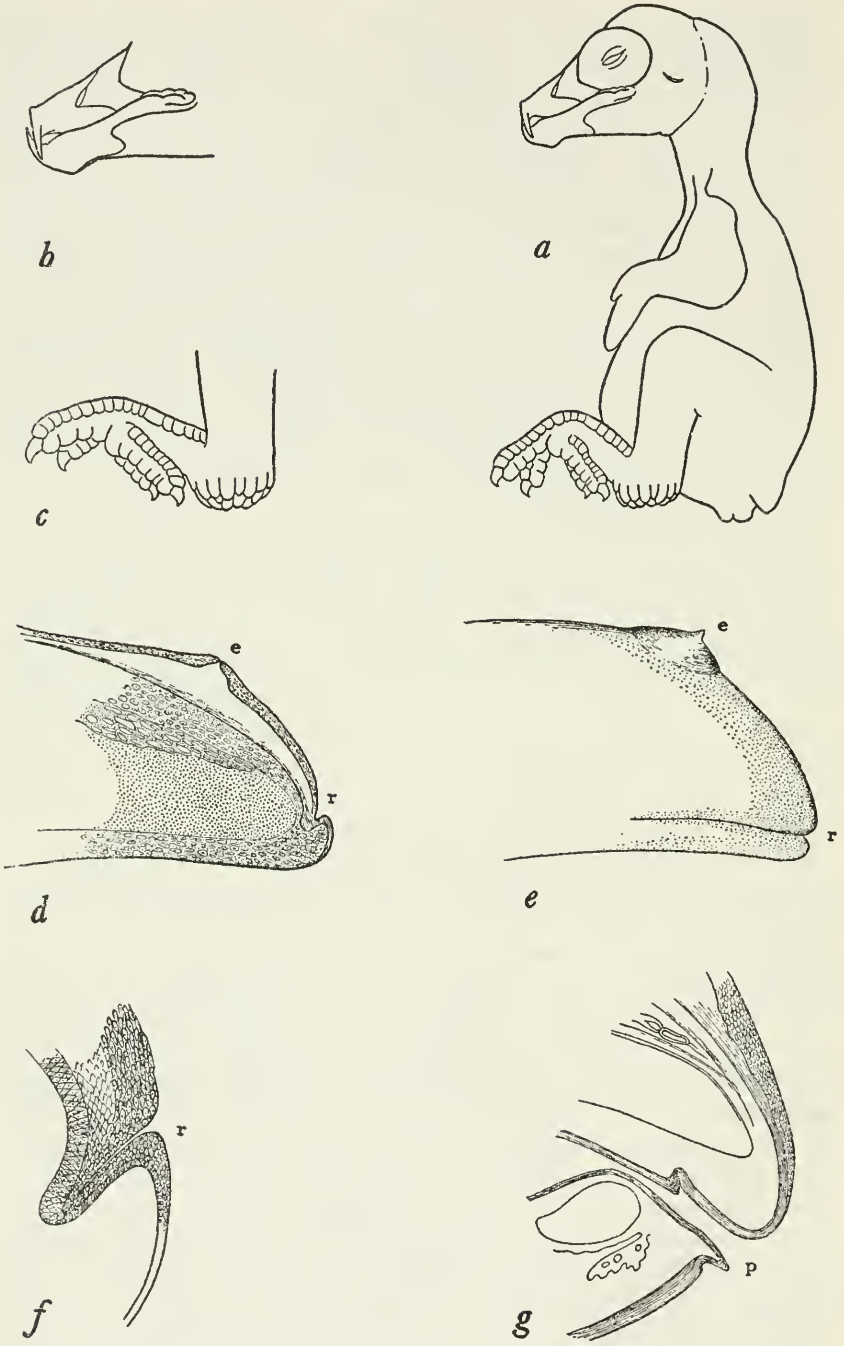
b
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Figure 4.—For explanation see opposite page.

tooth found in most birds, although the egg-tooth is usually found only on the maxilla and not necessarily at the extreme tip. Rosenstadt (1902, p. 511; 1912, p. 612) reports that the egg-tooth is formed embryologically on the lower mandible in the domestic chicken as well. Also, Willink (1899) writes that not a few genera of birds have such mandibular, in addition to maxillary, callosities. Among the genera he mentions are *Oedicnemus*, *Haematopus*, *Numenius*, *Limosa*, *Recurvirostra*, *Sterna*, *Otis*, and *Gallinula*. The mandibular callosity is generally less elevated and basally broader than the maxillary one.[4] To this list Stresemann (1928, p. 286) adds that in newly hatched loons (*Gavia*), hornbills (*Bucerotidae*), and some auks (*Alcidae*) the tip of the mandible, which protrudes beyond that of the maxilla, is hardened into a sharply pointed wedge in the form of an egg-tooth.

While these records are of interest in demonstrating that the condition of mandibular plus maxillary callosities does occur elsewhere in the avian class, these callosities are not extenuated and hooked, but blunt excrescences. Nothing of the sort appears to have been recorded for any other birds, but it may be recalled that in newly hatched woodpeckers, kingfishers, and jacamars the mandible often exceeds the maxilla in length, and the maxilla is often curved downward slightly at the tip in some woodpeckers and puff-birds. Coming still closer to the honey-guides in systematic position, in newly hatched prong-billed barbets, *Dicrorhynchus frantzii*, Skutch (1944, p. 75) found that "the lower mandibles of their short bills were both longer and broader than the upper mandibles, as in newly hatched woodpeckers, toucans, and kingfishers. Their egg-teeth were less prominent than those of woodpeckers." The Heinroths (1926, p. 321) describe the egg-tooth of the black woodpecker, *Dryocopus martius*, as a singular, highly peculiar structure on the tip of the maxilla, formed like a peak of an elongated cap on the tip, contrasting sharply in its whiteness from the rosy color of the rest of the bill. No specific mention is made to the effect that the tip of the mandible is equally as hard as the maxillary callosity, but it is suggested by inference rather than by actual statement that the two are similar.

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[4] Curiously enough, Willink's study appears to have been stimulated by Weinland's unreliable record (Proc. Essex Inst. (1856–60), vol. 2), p. 115, 1862) of double egg-teeth in *Ereunetes pusillus*. What bird Weinland had is not clear, but inasmuch as it was collected a few days after hatching at Nahant, Massachusetts, it could not have been this sandpiper, which does not breed within many hundreds of miles of that area.

FIGURE 4.—*a–c*, Outline drawing of 2-day old greater honey-guide, ×2, showing bill hooks (*b*), ×3, and heel pad (*c*), ×3. *d*, Longitudinal section of bill of 14-day chick embryo (ex Gardiner), showing egg tooth (e) and oral groove (r). *e*, Oral groove in a somewhat older chick embryo (ex Gardiner). *f*, Bill of an 18-day chick embryo (ex Gardiner). *g*, Longitudinal section of bill of *Milvus* embryo (ex Gardiner), showing mandibular papillum (p).

In this connection, I examined alcoholic specimens of nestlings of several species of woodpeckers (*Colaptes auratus*, *Picoides tridactylus*, and *Dendrocopos pubescens*) and one barbet (*Megalaima asiatica*). The barbet showed no sign of any mandibular callosity, but had the short, somewhat upturned symphesis of the two rami hard, like the maxillary egg-tooth and cap (the rest of the bill being softer) and terminating in a sharp point, in this respect not wholly unreminiscent of the sharp mandibular hook of *Indicator indicator* and of *I. minor*. This point, it must be emphasized, was not an extension from the mandible but merely the form of the gonydeal edge of the union of the two mandibular rami; it could be distinguished more readily by touching with the finger than it could be seen even with a hand lens. In two examples of the three-toed woodpecker, *Picoides tridactylus*, the tip of the maxilla was white and hard with a small egg-tooth on the middorsal ridge just where the tip itself turned down a little; the mandible was noticeably longer and had its ramial symphysis similarly hard and whitish and very slightly upturned. This condition was also found in two specimens of the flicker, *Colaptes auratus*, and in three downy woodpecker chicks, *Dendrocopos pubescens*. In all three species the upward terminal inflection of the mandible and the downward curvature of the maxilla just at the locus of the egg-tooth can easily be overlooked; they are not sizable, conspicuous features and consequently they have gone almost unnoticed in the literature of these birds. The hooks of *Indicator* chicks are not too different in kind from these beginnings. Chapin (1924, p. 335) has suggested that these hooks may be "homologous with the extensive calcareous cap which at first covers the entire tip of the upper mandible of young woodpeckers." Our present examination bears this out.

Thus, while there is some evidence for the occurrence, elsewhere among birds, of double bill callosities, it remains that the condition found in the honey-guides is unique. We need much more information on the bills of newly hatched honey-guides of other species and genera before we can hope to enlarge our understanding of this phenomenon, but it appears to be a specialization of such a degree as to argue for the great antiquity of the mode of life towards which it is an adaption. For a detailed description of the use of these hooks by the honey-guides, the reader is referred to the account of the nestling lesser honey-guide (p. 206).

The guiding habit

All the early accounts of the guiding habit, even when the species of honey-guide involved was not definitely stated, may safely be taken to refer to the greater honey-guide. As will be seen, these early records of our pioneering predecessors, while historically interesting, appear to be based to a very large extent on information gathered from the natives rather than on the personal experience of their narrators.

History of our knowledge of the habit

The earliest reference known to me concerning the honey-guides and their habit of leading men to bees' nests is in a book entitled "Ethiopia Oriental" by João dos Santos, a Portuguese missionary to Sofala, in what is now Portuguese East Africa, first written in 1569 and printed in 1609. In that work the bird is discussed on pages 35, 36 under the marginal title "Sazu passaro que come cera" [Sazu, a bird that eats wax]; sazu being the local native name for the two common species, *I. indicator* and *I. minor*. It appears that this bird attracted the attention of the good padre because he noted it flying in through the open window into his mission church to feed on the bits of wax in the candlesticks on the altar.[5] In his account he tells us that the sazu frequents the woods in search of bees' nests, which are very numerous both in holes in the ground and in the trunks of trees, and says that when the birds find a beehive they go to the roads in search of men and lead them to the hives by flying on before them, flapping their wings actively as they go from branch to branch, and giving their harsh cries. As soon as the natives notice the birds acting in this way they follow them, as they are very fond of honey. The profit that the birds reap from all this is that they feed on the small scraps and pieces of the honeycomb, wax, and the dead bees that are left when the natives get through robbing the hive.

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[5] Considering that the first observations of the greater honey-guide occurred in a missionary's little church, it is of interest to find nearly four centuries later that Charbonneau-Lassay (1940) suggested that the honey-guide (no specific identification but by inference the greater honey-guide) may figure in the symbolic iconography of the Catholic church in Abyssinia. He reasons that not only does the bird lead men to "sweetness" but also to bees, which in the Middle Ages were used as an example, especially to the friars and nuns, of an ideal life of communal industry and cenobitic chastity and, to a wider audience, as a symbol of the Resurrection. In one of his sermons, Peter of Capua refers to the risen Christ as "apis aetherea," while not infrequently the saints noted for good works were compared to bees. The usage implied by Charbonneau-Lassay seems to be based solely on the inclusion of the thought in a letter written by Leopold Martin (a member of the Order of St. Vincent de Paul and a missionary to Abyssinia at the beginning of the present century) addressed to a colleague, the Abbé Dury, curate of Chalais.

From the northern end of the bird's range comes the next observation, in Father Jerome Lobo's "Voyage to Abyssinia," written in Portuguese in 1659 but not printed until 1728, when it was brought out in French by Le Grand. It was translated into English in 1789 by no less famous a figure in English literature than the great lexicographer, Samuel Johnson. I quote from the latter's version of ". . . the Moroc, or honey-bird, which is furnished by nature with a peculiar instinct, or faculty of discovering honey. They have here multitudes of bees of various kinds . . . of the wild ones, some place their honey in hollow trees, others hide it in holes in the ground, which they cover so carefully, that though they are commonly in the highway, they are seldom found, unless by the Moroc's help; which, when he has discovered any honey, repairs immediately to the roadside, and when he sees a traveller, sings, and claps his wings; making many motions to invite him to follow him, and when he perceives him coming, flies before him from tree to tree, till he comes to the place where the bees have stored their treasure, and then begins to sing melodiously. The Abyssin takes the honey, without failing to leave part of it for the bird, to reward him for his information."

Johann Otto Helbigius (1680, p. 454), a German physician in the service of the Dutch East India Company in Batavia who went to Java via the Cape of Good Hope some time before 1677, published a brief statement of the bird's guiding habit but erroneously described the bird as green like a parrot. (I am indebted to Dr. Stresemann for calling this reference to my attention.)

Giovanni Antonio Cavazzi da Montecucculo (1687, pp. i, 59) refers to the honey-guide by the West African native appellation "sengo," and mentions that it leads natives to bees' nests.

Jobus Ludolphus (1682, translated by J. P.) describes the greater honey-guide under the local Abyssinian name of "pipi" as leading men to wild beasts, but notes that in Guinea, where it is called "fonton," it is reported to "betray not only Wild Beasts, but also Serpents and Bees."

In his "A Voyage to Congo . . . in the year 1682 . . .," Father Jerome Merolla da Sorrento (1744, p. 566) makes a brief mention of the greater honey-guide, and states that while it usually leads natives to honey it may at times lead them to a lion or other dangerous creature. Merolla's work is printed in English translation in Churchill's "A Collection of Voyages and Travels . . .," volume 1, 1744.

The next mention of the bird is again from southern Africa, in a letter written in 1695 by J. G. de Grevenbroek (in Schapera and Farrington, 1933, p. 177), who states he has observed that "Africans are led to the bees' nest by the song and flight of a certain little bird that is very fond of honey."

Peter Kolben (1731, pp. 154–155) gives a much garbled account of a bird referred to as the "gnat-snapper," which is evidently a compounded mixture of a honey-guide and a bee-eater. The fact that he writes that the bird guides the Hottentots to bees' nests shows that the gnat-snapper is based partly on *Indicator*, while the description—long red bill, blue feathers on the breast—suggests *Merops*. His crude black and white figure also suggests *Merops*. It has been reproduced by Seyffert (1930, p. 24) and by Bodenheimer (1951, p. 171).

Andrew Sparrman's account of the honey-guide, published in 1785 (vol. 2, pp. 186–193), is generally referred to as the starting point of our knowledge of the guiding habit, although he specifically makes reference to Father Lobo's account of some 57 years earlier. Sparrman is the first writer to inform us that not only does the honey-guide lead natives to bees' nests but that it does the same with ratels or honey-badgers. His account of the association of the bird with the ratel gives us no reason to assume that he had actually witnessed such cooperative action, and probably rests on tales reported to him by native informants.

Since Sparrman's time there have been published innumerable short notes and records of specimens, many of considerable interest, brief accounts of guiding experiences (usually devoid of any details which would have made them much more informative), incomplete compilations of existing data, and many accounts of the honey-guide and ratel story, all apparently based on earlier stories of other writers or on hearsay evidence only. While a considerable corpus of data could be gleaned from the total literature as recently as 1947, it was still very uneven and provided little as a basis for understanding and possible interpretation. At that time I prepared a fairly detailed list of questions for circulation among bird observers in Africa. This questionnaire yielded a good number of new observations of value and had as its most notable result a paper by C. J. Skead (1951) in which for the first time details of individual guiding experiences are set down with accuracy. The same author had published one earlier report (1946) giving detailed evidence on the circuitous route of one guiding experience that clearly demonstrated for the first time what has since been found to be generally characteristic of guiding.

Earlier explanations

As might be expected because of its unusual features, the guiding habit has elicited several explanations by various authors. While none of them are wholly satisfactory they deserve mention because of some of the facts and ideas they contain. The basis for most of them is the assumption that the bird derives a benefit from the habit in the form of otherwise inaccessible food thereby made available to it.

Seitz (1923, pp. 22–23) considers the relationship between the honey-guide and the ratel as something akin to the beginnings of domestication of animals, but does not attempt to theorize about the origin of the relationship.

Chapin (1924) suggests that the honey-guides would seem incapable of breaking open many bees' nests as their beaks are not well suited for such a purpose, and that their present feeding habits probably could not have developed without the aid of a collaborator, such as the ratel. The fact that many species of honey-guides feed on wax but do not guide certainly suggests that cerophagy developed before guiding, as the former is independent of and more widespread than the latter. Chapin suggests that the habit may have started by the birds finding ratels at newly demolished bees' nests and then, by a sort of mutual association, the two creatures becoming auxiliaries in their search for beehives. In the absence of further data it is not stated how the bird became the leader, and conversely, why and how the ratel, which apparently had been able to find and open bees' nests by itself previously, became a follower of the honey-guide. This gap in our understanding is not a weakness of Chapin's theory, which is fairly similar to that which I shall propose here, but is due to a lack of factual knowledge. The greater mobility of the bird may have caused it to go on ahead of its slower moving companion, and to wait for it to "catch up" at intervals. We have no data on the relative frequency with which ratels rob hives with and without the aid of the honey-guides.

Quite different is the suggestion put forth by Hoesch (1937), who feels that the guiding habit may have started between the honey-guide and the primitive African human, and that the fact that even the natives repeat the story of the ratel is due to a form of anthropomorphism of the savages themselves, although he admits that it is entirely conceivable that the sight of a ratel may also be as effective a releaser of guiding behavior by the *Indicator* as is the sight of a human. It should be kept in mind that Hoesch was overly impressed with the printed statements to the effect that the ratel was a wholly nocturnal and purely terrestrial creature, incapable of climbing. This would have made it improbable that it would get in touch with a diurnal creature like a honey-guide, and would have limited its activities to bees' nests in or on the ground, those in trees being thought out of its reach. Hoesch remarks that many creatures indicate, by their excited movements and calls, the presence of a snake or beast of prey, supposedly recognized by the bird as a dangerous enemy. Hoesch argues that originally the bees, because of their stings, were also regarded as "enemies" by the bird in the same sense, and that the honey-guides led men to these enemies, and only incidentally to honey and comb.

Although Hoesch's explanation is not convincing, it should be presented more fully in his own terms He explains that incidental or even only occasional meeting of the bird with a ratel at a bees' nest, even if it happened much less often than a joint arrival there by a human and the bird, might be sufficient to develop the memory capacity of the *Indicator* with respect to the ratel so as to cause the bird to react to it as it does to a human. But Hoesch finds it difficult to accept the idea that the ratel should be as suitable an object for such a symbiotic relationship as the savage human (assuming, as he does, that the latter was already on the scene when the habit started). He considers that the role a honey-guide might play in cooperation with a ratel cannot be very great for two reasons. Firstly, he assumes that if the collaboration were even partly to offset the bees as "enemies" from the birds' standpoint, the native human would be a better collaborator than a ratel inasmuch as the former would kill the bees or at least get rid of them by smoking them out while the ratel would do neither, but, on the contrary, might cause the bees to become more excited and aggressive towards itself and its avian accomplice. This is a highly speculative assumption and does not carry any real conviction. Secondly, he assumes that after a ratel finished its meal at a bees' nest it would be only a lucky accident if anything was left for the bird. This suggests very clearly that he never saw a bees' nest after its demolition or he would have noted the strewn bits of comb left lying all about. Hoesch writes further that the fact that *Indicator* does sometimes (he writes "frequently") lead men to large beasts of prey or to snakes instead of to bees seems to signify that in both cases what the bird is doing is only to lead one to an enemy.

While this conclusion may be safely dismissed on the basis of many data presented in our discussion of the guiding habit, a further point elaborated by Hoesch deserves mention, even though it too seems erroneous. He points out that the behavior of the honey-guide is peculiar [6] in that it not only announces or indicates but also leads or guides, and that the human is in the position of releasing the reactions of both announcing and leading. Cases of simple announcing are quite numerous in animals, even though the individual instances may be difficult to explain. A great many small birds announce or indicate by their actions to other creatures, including man, the presence of a dangerous beast just as they may reveal the presence of a stalking hunter to his otherwise unsuspecting quarry. But the idea of leading humans to something is strange, especially when one considers the common tendency of birds to lead one away from something—from a nest, from their young, etc. The only instance Hoesch could recall of a bird leading to something was an experience in which two rollers (*Coracias mozambicus*) led him with excited cries about 300 meters to a genet caught in a trap, and he stresses that in this incident there were two things of note: a goal or object to which the leading was directed, and a human that was the releasing object of this behavior. From this case and from a rather superficial acquaintance with the guiding behavior of the honey-guide, Hoesch's thinking apparently was oriented towards the conclusion that guiding is, or originally was, basically a matter of leading a human to a dangerous enemy whose presence caused a state of excitement in the guide.

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[6] Maclaud (1906, pp. 123–124) writes that a bulbul, *Baeopogon indicator*, shows the natives the location of wild bees' nests, and after the Negroes have taken the honey the bird feeds on the larvae in the comb! This is, of course, an error, the habit of *Indicator indicator* being here transposed to the account of a similarly colored (and named) bulbul.

While the case of the rollers leading to a trapped genet may well be correctly presented and interpreted, it is not admissible to carry this reasoning over into the ordinary guiding to a bees' nest. As we shall see later, when the guiding bird begins to lead it does not necessarily, or even frequently, know where it is going to stop. There is no reason for assuming that it always has any conscious goal. Furthermore, Hoesch's exposition makes the matter of "announcing" or "indicating" the presence of something the end, or the basic portion, of the habit, while "leading" or "guiding" a follower to this object is merely a means to the end. The actual behavior of the honey-guide is, however, quite different. After all the effort and excitement of "guiding," the bird often merely becomes quiet and silent when it nears the goal. As far as direct, unaided observation of the bird goes, there is no indication of any increase in tension or excitation as the "goal" is approached; frequently quite the opposite Hoesch's whole discussion seems to have no basis in familiarity with the guiding habit at first hand, and, indeed, in the report by Niethammer and himself the species *Indicator indicator* is not even listed.

Recently Toschi (1949, pp. 12–17) discussed the subject and considered that the guiding behavior was not unique but partook of the same elements as the alarm reactions with which small birds indicate the presence of enemies, thus agreeing in his basic considerations with Hoesch, of whose paper he appears to be unaware. Toschi's presentation is less coherent and less convincing than Hoesch's, but he concludes with a statement to the effect that a beehive with its numerous individuals may be an entity of considerable significance in the ecology of an African forest, and may cause reactions and stimuli on the part of small birds similar to those that are otherwise provoked by the passage of a lion through the grass or the presence of a leopard crouching in a tree. He thinks that the beehive represents, ab initio, something in addition to, and different from, food in the form of honey and comb. Just what it represents he prefers not to say in the absence of fuller information, but he definitely relates the guiding to bees' nests to the fact that the guide sometimes may lead one to a wild beast.

In view of the fact that Toschi's discussion remains on a very conjectural plane it is not possible to criticize it in detail. His attempt to reduce the seeming uniqueness of the guiding habit in birds is laudable in intent but it cannot be called successful unless one is willing to go along with him on the intangible assumption that the beehive had another meaning than as a source of food, but with this "other meaning" left undefined and undescribed. Some years earlier than Toschi another Italian naturalist, Fossati (1936), made a similar attempt to reduce guiding to a common denominator with alarm reactions, likewise overlooking the fact that if it were to be so interpreted we would have to accept the difficult picture of a bird giving a specialized alarm reaction concerning an object it cannot see and whose position may even be unknown to it at the time.

Native legends

While no serious attempt has been made to collect native legends about honey-guides (apparently they chiefly concern one species, the greater honey-guide), the following few may give some idea of their variety.

Natives often make use of the fact that very occasionally a honey-guide may appear to lead to a dangerous animal instead of a bees' nest, to impute a revenge motive to the bird. This has given rise to a variety of proverbs, such as:

If you do not leave anything for the guide, it will lead you to a dangerous animal the next time.

If you do not leave anything for the guide, it will not lead you at all in the future.

If you do not leave anything for the guide, it will come to you and chatter when you are stalking game, and thus reveal your presence to the intended quarry.

A contrary proverb says in effect that if you give the bird too much food it will not guide again for such time as the food supply lasts, and that, therefore it is unwise to leave much for it.

A peculiar attempted explanation of the guiding habit is to be found in a Rhodesian native fable (J. D. Roberts, African (Rhodesian) Fables). It appears that once upon a time a honey-guide came upon a dead elephant. "Ha," he said, "this is going to be my new home." He was happy about finding so much food, and then thought of calling his relatives and friends. So he made a mark on the carcass and went off to tell them about it. In his absence a mouse found the elephant and also decided to make his home there, and began to nibble away at the huge body. On his return with his friends, the bird saw that the mouse had installed himself, and tried to evict him, saying, "This is my place." The mouse replied, "No, it is mine." They then fought over it, and afterwards decided to take the matter to a judge, who happened to be a bee. The bee said, "It is the mouse's food." The bird argued that he had found it first and called attention to the mark he had made on it before the mouse came. The judge said "You are lying; it is the mouse's property." From that day to the present the honey-guides and bees hate each other, and that is why the birds lead men to destroy the bees' nests.

The Bambemba, a Bantu tribe in the Northern Province of Northern Rhodesia, carry the heart of a honey-guide with other medicines in a horn when looking for honey (Brelsford, 1941). Many tribes will not kill a honey-guide, and formerly inflicted severe penalties for such an act, but it would seem that the Bambemba may do so to obtain the heart.

Typical guiding behavior [7]

When the bird is ready to begin guiding it either comes to a person and starts a repetitive series of churring notes or it stays where it is and begins calling these notes and waits for the human to approch it more closely. These churring notes are very similar to the sound made by shaking a partly full, small matchbox rapidly lengthwise. If the bird comes to the person to start leading him, it flies about within 15 to 50 feet from him, calling constantly, and fanning its tail, displaying the white outer rectrices. If it waits for the potential follower to approach it for the trip to begin, it usually perches on a fairly conspicuous branch, churring rapidly, fanning its tail, and slightly arching and ruffling its wings so that at times its yellow "shoulder" bands are visible. As the person comes to within 15 to 50 feet from it, the bird flies off with an initial conspicuous downward dip, with its lateral rectrices widely spread, and then goes off to another tree, not necessarily in sight of the follower, in fact more often out of sight than not. Then it waits there, churring loudly until the follower again nears it, when the action is repeated. This goes on until the vicinity of a bee's nest is reached. Here the bird often (usually, in my experience) suddenly ceases calling and perches quietly in a tree nearby. Some observers record no such cessation of the churring notes when near the bees' nest, but all agree that the bird perches unobtrusively in a nearby tree or shrub and there waits for the follower to open the hive, and it usually remains there until the person has departed with his loot of honeycomb, when it comes down to the plundered bees' nest and begins to feed on the bits of comb left strewn about. The time during which the bird may wait quietly may vary from a few minutes to well over an hour and a half.

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[7] By "typical" behavior is meant behavior when leading a human being; we still have no detailed data on the behavior when leading a ratel, but there is no reason for assuming any very significant difference. The data here given refer to *Indicator indicator*.

I know of no reliable evidence supporting the contention that the honey-guide necessarily leads only to nests of certain kinds of bees and not of others. Yet such has been claimed by a few writers. Hughes (1933, p. 335) states that the birds seem to ignore the nests of certain tiny black bees (not identified) which usually are found in the hollow knots in trees and readily spotted by the thick, black streak trailing down beneath the opening. Bodenheimer (1951, pp. 180–181), referring to this account and also to one by Marais, mentions two kinds of bees in the northern Transvaal. One of these, *Trigora clypeata* Friese, lives in very hard, virtually impenetrable soil. "Even the honey-guide, partial to wax, does not lead his allies to the ground or arboreal nests of wild bees." What Marais (1912) actually says is that "stingless as they are, the Moka bees are well protected against all honey-thieves, and especially against man and the ratel. The honey-bird never leads to one of their hives." Both Hughes and Marais seem to be writing loosely; their statements lack the corroborating details necessary to transform them into evidence.

Guiding is usually done by one bird; in fact, of all the literally hundreds of individual guidings that I have been told about or have read of, I know of only a small number of instances where two birds were involved jointly prior to the arrival at the bees' nest by the guiding bird. Mr. Will Foster, Superintendent of the Umfolozi Reserve, Zululand, tells me that once he was guided by two birds which appeared to be "working together"; unfortunately, he noted nothing further about them. Mr. E. M. North, Makueni, Kenya Colony, writes me that he was once followed by a pair of adult birds for about half a mile (about 10 minutes) that were trying to get him to leave his work and follow them. These two birds arrived and remained together throughout this period (about 10 minutes), at the end of which time North rejoined his lorry without having the time to follow the honey-guides.

A third case is one reported by Chapin (1939) in the Belgian Congo, near Faradje, in November. He and his native assistants were following a guiding male when "another male joined him. We had gone about 600 yards when both birds stopped in a tree . . . . The buzzing of passing bees was now traced to a small hole in the ground close by . . . . We prepared to make a fire, and our birds retired noiselessly for the time . . . . They seemed to be quarreling, and one soon chased his rival off at top speed."

A fourth case, quite similar to Chapin's experience, is one related to me by Dr. W. Büttiker, then of Salisbury, Southern Rhodesia. On February 20, 1951, he was led by a greater honey-guide a distance of 429 yards to a wild bees' nest. For the last 200 yards of this trip a second bird joined in. When they arrived at the vicinity of the nest, which was in an old termite mound, each bird went to a separate small tree, about 6 yards apart, and quieted down for a moment. Then the second bird attempted to chase the first one, but the latter drove off the former individual, which then went on farther ahead by itself. For lack of time, Dr. Büttiker was unable to follow the second bird. In response to further inquiry, Dr. Büttiker writes that it is "difficult to say whether the two birds acted in unison. It seemed to me that No. 1 was the leader and No. 2 intended to guide to another bees' nest . . . . As the first bird arrived at the ant-heap the second arrived a few seconds afterwards, quieted down a little and then soon began to fight with No. 1. The fighting lasted not more than 1–2 minutes and it was not carried out continuously. The two birds watched me from the two separate trees when I was busy watching the bees flying in and out." Another observation in Southern Rhodesia comes to me from Neuby-Varty (in litt.). On January 9, 1952, he was led by a greater honey-guide for about half a mile when a second bird started to give the chatter note; when he got close to them the two birds flew off together and settled in the same tree, but only one called; they did this three times and then one just flew away leaving the original (?) one, which lead him to a bees' nest. Both birds were adult males, making it difficult to be certain that the bird that completed the guiding trip was the same individual that started it, but I am informed that the observer thought that it was.

The only other instances known to me took place in Kenya Colony. At Nyeri, Lt. Col. C. H. Stockley saw what he took to be a pair of greater honey-guides (in his letter he gives no details as to whether they were merely two individuals of unobserved sex or if they were actually one male and one female) and was led by them to one of his own hives. This was the only time he ever saw more than one honey-guide at a time. Jackson (1938, p. 732) was once called by two birds while hunting.

Mr. John G. Williams, of the Coryndon Museum, Nairobi, writes me that he has followed honey-guides at least 30 or 40 times and that the initial guiding was almost always done by one bird, but in two or three cases "a pair of birds—male and female—would start their excited chatter, and both commence to guide in the same direction, following one another from tree to tree. However, in the majority of cases it was just the one bird which guided to the bees' nest, but it was not uncommon for this one bird's chattering to attract a second bird, as often as not of the same sex, when one drew near to the bees' nest, and on a few occasions a third bird was also drawn by the chattering. The appearances of the second and the third birds were almost always in the vicinity of the bees' nest."

Jackson (1913) was once stalking buffalo when two honey-guides began to chatter near him. When he had gone perhaps 200 yards farther, three of these birds became very noisy. He does not say, however, if the original two were included in the three, and in this instance no guiding ensued, as his shooting scared off the birds.

My own experiences with the guiding habit (23 cases) have always been with single birds. On one occasion, in Zululand, what I took to be a second honey-guide flew across the path of the guiding bird but did not linger or attempt to join it.

Although there is ordinarily but one honey-guide doing the guiding, not infrequently another individual may come to the bees' nest after it has been opened and robbed, and then feed there with the guiding individual. On the few such occasions on which I have any notes, there was no indication of "possessiveness" on the part of the guiding bird or of "rivalry" or "hostility" between it and the other bird or birds feeding on the spoils. In some cases these extra birds have been of the opposite sex; in other cases they have been found to be of the same sex. In at least one case, in Kenya Colony, communicated to me by J. G. Williams, not only did another *I. indicator* come to the opened hive to feed, but a lesser honey-guide, *I. minor*, also joined them. In the eastern Cape Province, Ranger has found these two species coming together at bees' nests, and has seen as many as five and even six of them at one time at a hive. Once he saw two variegated honey-guides together with a lesser honey-guide at a bees' nest. However, in many cases it seems that only the guiding individual feeds at the bees' nest, at least in the first minutes after the human accomplices have left.

The fact that usually only one bird is involved in any single guiding trip but that others may join it at the opened bees' nest suggests that these others (and possibly still other individuals) probably may hear and recognize the guiding calls but do not try to intrude before the goal is reached. This, in turn, suggests that usually there seems to be nothing in the guiding behavior, either visually or audibly, that acts as a releaser of like behavior in these other individuals.

Guiding is done by adult males, adult females, and by immature or subadult birds (yellow-throated plumage) presumably of either sex; however, the two immature birds actually collected while guiding have turned out to be males—one record of J. G. Williams in Kenya Colony, and one of my own in Natal. There is great divergence in the relative frequency of guiding by male, female, old, and young birds in the experience of different observers. Thus Capt. H. B. Potter, with some 40 or more years of living in the bush in Zululand and watching the birds and the game, was inclined to think that in far more of his innumerable guiding experiences he was led by males than by females, and almost all the leaders were adults. Unfortunately, he had kept no notes and was relying on memory. While modestly disclaiming for his impressions any value as evidence because of the lack of notes, he mentioned that guiding had seemed to him to be indulged in more frequently during the early part of the birds' breeding season and he had wondered if, in some admittedly unexplained fashion, it might even be akin to a display on the part of the male. While this would seem to be negatived by the fact that guiding has been recorded throughout all times of the year and by the fact that guiding birds are usually lone individuals, the thought reflects the apparent predominance of males doing the guiding.

In the eastern Cape Province Skead (1951) records being guided by both sexes, but at that time had never encountered an immature bird guiding. Later, during a fortnight that Skead, Gordon A. Ranger, and I spent in the bushveld near Kei Road studying honey-guides intensively, Ranger and I found that all the recorded guiding in the valley in which we were camped was done by immature birds. Ranger was of the opinion that this predominance of subadult birds doing the guiding agreed with his previous long experience there. In a nearby area, Bedford, Victor Pringle writes me that he has been guided frequently by adult males, only once by an immature bird, and never, to his knowledge, by adult females.

My own experience in Natal and Zululand was as follows: Out of 14 times that I was guided by greater honey-guides, 2 were by adult males, 2 by adult females, and 10 by subadult birds.

J. G. Williams, Nairobi, summarizes his experience as follows: Adult males and females indulge in the guiding habit equally commonly; only once has he been guided by an immature bird. In the Mara River area, Kenya Colony, where *Indicator indicator* is most common, he never saw a subadult bird attempting to guide, although he did notice them coming down to feed with the guiding bird at the bees' nest after it had been chopped open.

In Northern Rhodesia, Maj. E. L. Haydock tells me that he has been led on numerous occasions, and that four specimens shot on these "leads" have all proved to be females.

That immature birds have been known to guide in northeastern and eastern Africa is attested by the fact that many years ago von Heuglin (1869, pp. 767–769) described *Indicator major* (=young *I. indicator*) as guiding in the same way as *I. indicator*, which was then thought to be a different species. Furthermore, Mackworth-Praed (1917, p. 392) was led to a bees' nest by a yellow-throated honey-guide at Tsavo, Kenya Colony.

While the above data clearly show that males and females and old and immature birds do guide, there is some evidence to account for the unusually high percentage of guiding by immature birds in the experience of Skead, Ranger, and myself. A good part of our cases were recorded in a bushveld area (Umtaleni Valley) near Kei Road. In this area the adult male honey-guides were definitely established on "call sites" (or, as we came to call them, "stud posts") to which they adhered from 8 a. m. to 4 p. m. not only during the breeding season but throughout much of the year, and from which they would not be lured away to guide us. This immobilization of the adult males may be reflected in the high incidence of subadults among the guiders. Study of long series of museum specimens also indicates that the yellow-throated plumage is retained until the birds are two years old, although they begin to breed when one year old, a fact that also helps to swell the number of subadult birds recorded. This situation should, however, be examined elsewhere over the range of *Indicator indicator*, and similar tallies may be expected with more resident observers.

While some observers have informed me that they considered guiding somewhat seasonal, none have claimed more than that its frequency was greater at one time of the year than another. The accounts received from men in the field and from the literature, as well as personal experience, do not justify any attempt to correlate the habit with the season of the year or the breeding condition of the birds. This is most clearly shown in southern Africa where the seasons are more definite than in the equatorial portions of the continent. My own experience there happens to have been quite seasonal—end of winter (late August) to late summer (third week in January)—and I have been guided by nonbreeding as well as breeding birds in August, September, October, November, and December. Resident observers such as Skead (1951) have been guided in May, June, July, August, and November, and there are records for guidings in South Africa for January, February, and March as well. In other words, there are records of guiding throughout the year in South Africa.

It is only fair to include observations of those who consider there is some seasonal correlation. Thus, Capt. H. B. Potter, of the Hluhluwe Reserve, was of the opinion that guiding in Zululand was chiefly indulged in during the time when the birds were breeding—October to January. On the other hand, Will Foster, of the Umfolozi Reserve nearby in Zululand, thought the birds guided mostly in the winter (May to August) but on further questioning admitted that he noticed the birds mostly in the winter because that was when he did most of his hunting. However, it is obvious from the evidence of these two men in the same general area that guiding was done throughout the year.

In Upemba Park, southern Belgian Congo, Verheyen (1951, p. 49) found guiding to be seasonal, depending, apparently, on the flowering of the vegetation, which, in turn, affects the activities of the bees. It seems from his description that in the xerophitic woodlands of the Katanga the efflorescence of the trees and shrubs is seasonally restricted in very marked and striking fashion. Verheyen's experience, based on two years residence, cannot be brushed aside easily, yet it is so out of keeping with the bulk of data from other parts of the continent that I cannot look upon it as more than a local situation and not as clear cut even there as he suggests.

Judging by negative evidence only, Lynes (1925, p. 352) wondered whether the absence of guiding behavior in Darfur from May to August might have been correlated with the fact that the honey-guides were not in breeding condition at the time.

Evidence of the nonseasonal nature of the guiding habit in East Africa comes from J. G. Williams, who informs me that he has been guided in Tanganyika Territory at the start of the rains and on the Mara River, Kenya Colony, during the dry season. He collected two adult guiding individuals and found that one, a female, was in full breeding condition, and the other, a male, had the testes quite small—obviously not a bird in breeding condition.

Other field naturalists in various parts of Africa have sent me similar statements, the total of which indicates that guiding is done throughout the year.

Guiding is done to bee's nests that are full of food and also to new and as yet empty nests, provided bees are flying in and out. In the Umfolozi Reserve, Zululand, Will Foster, the superintendent, reports that a greater honey-guide tried to lead him to a bee's nest which had been begun in a corner of his house just two days before. The nest was still empty.

Guiding may be done at times to bees' nests that are exposed, and in which the bird could get at the comb without the aid of a follower.

Guiding seems not to be recorded to old nests deserted by the bees even though some of them may contain considerable amounts of wax and other food.

Guiding may cover a duration of from a few seconds to half an hour, or possibly even an hour, and may involve a distance of from a few feet to over half a mile, and possibly, at times, even a mile. Skead (1951, pp. 59–60) has put on record the following data on six guiding experiences: One trip covered 20 yards in 3 minutes; another, 20–30 yards in 5 minutes; another, 100 yards in 20 minutes; another, 320 yards in 10–15 minutes; one, 100 yards in 4 minutes; and one involved no appreciable distance or time as the bird merely gave the guiding chatter call, flew off, and then returned to its original perch, which was close to a bees' nest. My personal experience includes 23 guiding trips (tabulated below). The longest one covered 750 yards and lasted 28 minutes, several were from 250–350 yards and lasted from 9 to 16 minutes; and the shortest one involved a distance of 20 yards in 2 minutes.

GUIDING TRIPS WITH INDICATOR INDICATOR

Time of day	*Distance, in yards*	*Time, in minutes*	*Number of stops*	*Age and sex of bird*
a. m.				
7:20	330	16	12	adult ♂
7:21	100	8	8	immature
7:35	120	10	7	immature
8:01	35	5	5	immature
8:05	250	9	10	adult ♀
8:05	750	28	16	adult ♂
8:08	350	15	10	immature
8:10	20	2	3	immature
8:35	50	4	3	adult ♂
8:35	130	10	5	immature
8:40	450	20	15	adult ♀
8:45	200	8	8	adult ♂
9:05	175	8	7	immature
9:10	75	4	5	adult ♀
9:30	150	7	7	immature
10:05	230	10	10	immature
10:45	100	7	5	adult ♂
11:20	80	5	5	immature
11:40	130	8	6	immature
p. m.				
3:15	175	8	6	immature
3:35	250	10	9	adult ♀
3:50	80	5	3	immature
4:35	100	6	6	adult ♂

Guiding is effected more by sound than by sight, but both elements enter into it. It is true, however, that the guiding bird is actually out of sight of the human follower most of the time—except on trips of very short duration. This was not only true in most of my own experiences but has been reported and commented on by several other observers.

Guiding apparently is not the chief food-getting method of *Indicator indicator*, as the bird does not seem to guide often enough for that even in areas where guiding is frequent. Furthermore, as the nonguiding species of honey-guides usually have beeswax in their gizzards (except for the genus *Prodotiscus*), it follows that wax is obtainable without guiding.

Guiding leads to the vicinity of a bees' nest, not to the exact spot; that is, the bird usually does not actually touch or otherwise indicate the exact location of the nest. There are many stories to the effect that if the follower is unable to find the nest the bird will fly directly to it, or will point to it with its bill, but none of these accounts are acceptable as accurate or are supported by detailed data.

Guiding is not instigated by hunger or by lack of wax, as shown by the full gizzards of birds shot while guiding.

Guiding is done at different times of the day, but chiefly in the morning; not at all at night. In the Hluhluwe Reserve, Zululand, I made several prolonged fruitless searches for honey-guides at and just after dusk—my reasoning based on the then not dispelled notion that the ratel was a wholly nocturnal animal and yet was associated with the honey-guide in its foraging.

Quite probably, in some and possibly in many cases, the guiding bird may not know in advance the location of the bees' nest to which it eventually "leads" its follower (see p. 59). It is true that in other cases the hives may have been known to the bird from previous experience, but it appears that this knowledge is not essential.

Occasionally one bird may lead a human follower to several bees' nests, one after the other, on the same trip. On these occasions there is, however, a definite pause or break at each nest, and the trip would probably not continue beyond such a break if the follower showed the proper interest in the nest and tried to open it.

The honey-guide often will come to a person or group of people to "lead" them, but at times will merely chatter where it is until the persons have come to it, whereupon it begins to lead them. The former seems to be the more frequent behavior, but this may be due to the fact that many cases of the latter type are left unnoticed because the persons do not bother to go to the chattering bird.

If a person does not follow a honey-guide that has apparently come to "lead" him, the bird may increase the tempo and excitement of its behavior as if to urge and entice, or it may give up easily and leave. No critical data are available as to why this activity may vary from individual to individual and from time to time.

A would-be "guiding" bird may sometimes follow a person for a very long distance (five miles is the maximum known to me) or for a very considerable period of time (half an hour is the maximum I know of) to attempt to get him to follow it.

The greater honey-guide leads ratels, baboons (data still very meager), and humans to bees' nests. It occasionally, but without success, attempts to get other animals—such as a monkey or mongoose—to follow. Because of the biological interest in this symbiotic relationship, a full discussion is in order here.

Mammalian symbionts

Number and kinds of symbionts: Guiding implies the existence and presence of something to be guided, or a follower that might be termed, from the standpoint of the biological end served by the habit, a temporary foraging symbiont.[8] Because of the complexity of the habit and all that its survival value (as distinct from its individual enactment) implies, it seems probable that a very considerable time span must have been involved in its development. This, in turn, suggests that there was a "co-operator," or a "follower," before the native African human associated himself with the bird in the finding of honey.

Many authors have written that the ratel or honey-badger (*Mellivora capensis*) is the original associate of the honey-guide in these quests for bees' nests, and that the natives (and, from them, Europeans) have stumbled onto the advantage of following the birds from seeing ratels doing so. However, in spite of the vividness and elaboration of some of these descriptions, none of the writers seems actually to have witnessed the association between the honey-guide and the ratel, but all have, often unwittingly, based their accounts on those of earlier writers, the eventual source for all of them being Sparrman (1785), who appears to have received his data from the natives and not from personal observation.

Sparrman did not attempt more than to record the story without embellishing it, but later writers have added to it. Perhaps the most detailed of these more recent descriptions is that given by Stevenson-Hamilton (1947, p. 242). This account reads as though it may have been based on personal observation, although no definite statement to that effect is made, and no such conclusion can be deduced from it.

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[8] This term seems better than what van Beneden (1876) would have called a "free messmate."

The fact that the association of the ratel with the honey-guide is reported consistently by the natives throughout vast portions of southern and eastern Africa is in itself suggestive of the factual basis of Sparrman's account, but by itself cannot be looked upon as constituting definite proof, even though at times the details are very suggestive. For example, I once asked a Zulu, who was helping me look for honey-guides, why he kept making grunting noises, to which he replied that it helped attract the birds. Some minutes later, after deliberately talking about other things to break the chain of thought, I suddenly asked him what a ratel sounded like, and without a second's hesitation or reflection, he replied "Just like a native calling to a honey-guide." This certainly suggested that the natives had patterned their "honey-guide technique" on an earlier model, and, to that extent, was evidence that there had been an earlier model.

There were two difficulties in the way of accepting the ratel story, both based on the habits of this mammal as recorded in the literature. In the first place, the ratel is said to be largely nocturnal, while the bird is strictly a diurnal species, and the inference would be that the two would have only a very brief period at dawn and at dusk when they might get together. Secondly, a good percentage of the bees' nests to which men have been guided by the birds were well up in trees, and as the ratel is said to be unable to climb, it would be a little difficult to account for the lack of discrimination on the bird's part between hives accessible and hives inaccessible to its associate, if the habit had developed with the ratel. I now know that both of these statements are only partly true; the ratel is diurnal to a fair degree in unspoiled areas, being partly nocturnal everywhere in its range, and almost entirely so now in areas where it has been disturbed. I also know of ratels climbing, although it is true that they are chiefly terrestrial. Thus, Maj. K. de P. Beaton (1949), warden of the Nairobi National Park, writes: "I have read that the ratel is unable to climb trees, but I do not believe this, for I have seen a native hive, which was placed in the branches of a tree, broken by one of these animals." Many years ago, Holden Bowker, a reliable observer in the eastern Cape Province, informed Dr. W. G. Atherstone that he shot a ratel robbing one of his beehives about 12 feet up in a tree. Bowker further told Atherstone that he thought the guiding habit of the honey-guide "probably originated with the ratel who climbs trees to get nests and leaves the comb scattered about where the Indicator eats either the grub or the wax" (in an unpublished notebook of Dr. Atherstone's, dated 1853, now in the Albany Museum, Grahamstown). Wilhelm (1950, p. 70–71) in South-West Africa, found the ratel frequently abroad in the daytime and found it climbed to and demolished bees' nests up in trees as well as those on or in the ground. Copley (1950, pp. 40–42) similarly notes that the ratel can climb, "perhaps not with the ease of a cat, but it attains its object, which is always a bees' nest."

However, when I went to Africa in 1950 I knew of no eye-witness account of this symbiotic relationship between the honey-badger and the honey-guide by a reliable European observer, or by a native known to be trustworthy in making such reports. Indeed, it was one of the main points on which I hoped to obtain some real information. The method used was the simple but time-consuming one of very extensive questioning both by personal conversation and by correspondence with "old timers"—farmers, game rangers, hunters, etc.—whose store of observations would otherwise remain unpublished and eventually might die with them. This was supplemented by searching through early archives in the main bibliographic repositories such as the Central African Archives in Salisbury, the library of the Africana Museum in Johannesburg, and the smaller collections in the libraries of Durban, Pietermaritzburg, King William's Town, and Bulawayo. The net result of all this searching was definite proof that the ratel does accompany the honey-guide to bees' nests, and that on such occasions the bird is the "guide" and the ratel is the "follower."

The first bit of evidence was supplied by Dr. John Hewitt. He found Dr. Atherstone's notebook in the Albany Museum in which it was recorded that an old Boer farmer named Oosthuizen, at Bushman's River, once "saw a ratel following a honey bird and make the same grunt that the Hottentot does." This evidence, welcome as it was, was not free of suspicion as it was quite possible that Oosthuizen may have been an uneducated man relating as a personal experience something that he had heard from the natives. This sort of conversational reporting is notoriously prone to such "enhancement" even among people aware of the importance of precise factual accuracy.

Major Beaton, in answer to an inquiry of mine, kindly supplied the next piece of evidence. He once actually saw a ratel and a honey-guide together in the Chepalungu forest, west of the Mau Escarpment, Kenya Colony. On this occasion, about 8 a. m., he was out hunting with a couple of his Wandorobo assistants when they heard a honey-guide chattering. The Wandorobo are very superstitious about this bird and think it may offend the gods who send it to guide them if they do not follow it, so the hunting was abandoned for the time being and Major Beaton and his boys pursued the sound. They soon found the bird perched in a tree about 30 feet high making a great chattering, and as they came nearer it remained in the tree and did not fly out as a guiding bird usually does. Coming still closer they heard the hum of bees close to the ground, and on peering into the undergrowth Major Beaton saw a native beehive (a hollowed log covered with bark) on the ground where it had fallen from above, and two ratels busily engaged in eating the contents. When the ratels saw Beaton and his boys they trotted off into the bush.

This observation, added to that of Oosthuizen, showed that ratels and honey-guides do associate at bees' nests, but there was no evidence that in Beaton's case the badgers had been led there by the bird. A third observation, supplementing Beaton's data and corroborating Oosthuizen's statement, came to me from Sir Robert C. Tredgold, Chief Justice of Southern Rhodesia, who told me that once at Inyati, about 40 miles from Salisbury, he was out in the bush at about 10 a. m. when he heard a grunting, growling sound and also the familiar chatter of a greater honey-guide. As he stopped and listened it came closer and closer until finally he saw an adult *Indicator indicator* definitely leading a ratel, which kept responding with a guttural growl every time the bird gave its chatter call. When the ratel spied him, however, it ran away, thus ending the episode without arriving at a bees' nest. Sir Robert also told me that he had known two native boys who had personally seen ratels following honey-guides. One of them in particular he praised as being a very observant and reliable naturalist. When asked if he considered their reports as constituting valid data, he replied that, after a lifetime of experience on the bench judging the truthfulness of native testimony, he had no hesitancy in accepting them.

E. L. Dutton, District Commissioner at Lundazi, Northern Rhodesia, writes me that he once observed a greater honey-guide leading a ratel near the edge of the Solwezi River at 6:30 a. m. in February. "While being led the ratel was extremely cautious and moved very slowly. The bird was very patient with him and not the usual impatient, vociferous . . . creature it ordinarily is. A native came too close to them and both disappeared."

Verheyen (1951, pp. 49, 91–93) also reports an eye-witness account of the ratel and honey-guide association in the Belgian Congo.

Thanks to the efforts of Mr. J. G. Williams, additional data on the association of the greater honey-guide with the ratel have come to me from several game wardens in Kenya Colony. These men, spending most of their time in the bush and having trained native game scouts of tested reliability reporting to them constantly, are in a very favorable position to gather and to evaluate such evidence. Mr. Roger A. F. Hurt, Game Department, Thomson's Falls, informs me that two of his native game scouts, whom he has found to be very reliable, have watched honey-guides calling to, and leading, ratels. His head game scout reports having seen this happen on three occasions, once at 8 a. m., once at midday, and once at 1 p. m. The other scout saw it but once—at midday. On each occasion the scouts were attracted to the scene by hearing the churring guiding call of the bird, and went to it in search of the honey themselves. They then saw that the bird was leading and calling to a ratel, and they followed at a short distance for some 200 to 300 yards until they came to the bees' nests. On two of these occasions the hives were in the ground, and on the other two in hollow trees. Once there was a pair (at least there were two individuals) of ratels, but in the other three occasions only a single ratel. The scouts never saw more than one honey-guide leading a ratel.

J. A. Hunter, game ranger at Makindu, writes me that his oldest scout, Malumbé, whom he considers a truthful and reliable reporter, once was led to a bees' nest by a honey-guide, and that a ratel, guided by another bird, arrived there at the same time from the opposite direction.

Recently I have been told by Dr. J. P. Chapin of two more Europeans who have reported to him that they witnessed ratels being led by honey-guides, one in the Ubangi-Shari district of French Equatorial Africa [9] and one in the region about 70 miles west of Namwala, Northern Rhodesia. It may now be considered as established that the tale first published by Sparrman, and since repeated over and over by others, is true. It may even be that some of the latter accounts were based on personal experience, although it was not possible to assume this before the validity of the story was proved by known eye-witness accounts. In addition to these it may be mentioned that several European naturalists resident in Africa have written me of their native assistants reporting seeing ratels following honey-guides. These cases were all voluntary, special reports by the natives of individual incidents and were not general statements of "nature lore" given in response to any questions put to them in my behalf.

The ratel is not the only mammal known to be associated with the greater honey-guide in the robbing of bees' nests. In Northern Rhodesia, Maj. E. L. Haydock was told by his native collectors that the bird also calls to baboons and monkeys, and that occasionally the baboons do follow it, but the monkeys never do. A corroborating and wholly independent bit of evidence came to me from the Cape Province, where Mr. Trevor McKenzie Crooks told me that one morning around Christmas time near Uitenhage he saw a baboon (one of a troop) opening a wild bees' nest with a greater honey-guide in attendance, chattering from a perch a little way up in a tree close to the hive. Crooks watched the procedure from a distance. The baboon first made a clearing by repeated short dashes towards the hive, which was low down in a soft-barked tree, until it had made more or less of a path. Then the baboon backed up to the tree and reached in with its hind foot, grabbed a piece of comb, and dashed off about 30 yards where it dropped it. Then, when the bees had calmed down, it came back to the piece of comb and cleaned it of bees by wiping it in the sandy ground, and frequently wiped its hands in the sand to get rid of the bees. It took Crooks about 15–20 minutes to get down from the krantz from which he watched this performance, and then the baboons (including the one that went to the hive) fled. The honey-guide stayed near the hive at his approach, and chattered to him. As far as Crooks could recall (the incident took place some years before he told it to me), the honey-guide was present before the baboon actually opened the hive; it did not come there attracted by the rending noises of the actual breaking open of the bees' nest.

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[9] This is apparently the case reported by Gromier (1938, pp. 135–139).

Major Haydock has generously given me still another observation of interest in this connection. Once, in Northern Rhodesia, he and his native assistants saw a greater honey-guide attempting to lead a small mongoose, *Myonax cauui lancasteri* Roberts. He first noticed the bird calling in the usual manner from a very small bush, about 4 feet high. At first he could not see what it was calling, but soon it flew to another equally small bush when Haydock was able to see the mongoose. The bird followed the mongoose, calling all the time. The latter stopped once and looked up, whereupon the calling was intensified, but the mongoose moved off without following. The bird then saw Haydock and began to focus its attentions on him and his natives, leading them to a bees' nest about 300 yards from that spot. The fact that a honey-guide would attempt to "guide" a nonfollower, such as a mongoose, suggests that the recognition by the bird of a potential foraging symbiont may partake of the nature of trial-and-error learning, although if this were basically the case one would expect more frequent errors of this sort. Indeed, from his experience in the Belgian Congo, Verheyen (1951, pp. 49, 91–93) suggests that the greater honey-guide "calls" to all the larger mammals, but his evidence is not conclusive and is contrary to the total experience of a great many observers in southern and eastern Africa. His assumption that the greater honey-guide does not distinguish between the various mammals is very doubtful.

No other creatures are known to be associated with the guiding behavior of the honey-guide, but it is not impossible that some others may be. Thus, Chapin (1939, p. 551) states that he finds it difficult "to abandon the idea that many species of Indicatoridae get help in attacking hives from squirrels, monkeys, or other mammals" since these birds are so poorly adapted, themselves, for securing what is known to be their usual food. There are no observations one way or the other, but it would seem plausible that the honey-guides might well find bees' nests that had been opened and robbed by squirrels, monkeys, or even hornbills, and might get some wax and food from them without having "guided" the predators to these spots in advance. On the other hand, Seitz (1923, pp. 22–23) goes so far as to say that in parts of Africa where ratels do not occur, "almost certainly" other mammals act in its stead.

Layard (1867, p. 242) tells us that "with respect to the oft-repeated story of the Honey-Guide leading persons to the nest of the honey-bee, it is as well to mention that the bird will perform the same antics, and utter the same cries, to lead anyone to a leopard, wild cat, or snake, or will even follow a dog with the same vociferations." His account does not make it clear if he actually witnessed a honey-guide following a dog but, if his statement is to be accepted as factual, it is conceivable that we may have here a case comparable to Haydock's observation of the bird attempting to "lead" a small mongoose.

Valence of the symbionts: In studying the guiding habit it is necessary to inquire as to the pertinent, common meanings of the various symbionts of the guiding bird. Only such values as are discernible in ratels, baboons, and humans are basic to our problem. The valence of these creatures, from the standpoint of the honey-guide, requires definition, description, and, if possible, explanation. To use the terminology put forth by Russell (1935), certain objects and events in an animal's environment that stand out as eliciting responses, as being apparently significant to the animal, are termed valent. The criterion of valence is simply behavioral response. It must be kept in mind that this "valence is not a quality of the object or event per se, but depends essentially on the needs and 'interests' of the animal; in this respect a valent object or event differs from a physico-chemical stimulus." Stating the same general thought in other words, Lack (1940a, p. 107) writes that to be effective a releaser must operate at a time when the internal state of the animal to be affected by it is in a proper phase for optimum response. The releaser in itself is not sufficient and, while it plays a directive role, the animal seems to react first to a more general situation. It behooves us to see how accurately and explicitly we may distinguish between the releasers and the general situation necessary for their effective operation; indeed, without such discrimination we cannot hope to get very far.

This brings us to the following point: Greater honey-guides of either sex, adult or immature, in breeding condition or not, at any time of the year and at any time of the day (not the night), hungry or with well-filled gizzards, are in a physiological or psychological state to be affected by the symbionts that release the behavior we know as guiding, or, to use Thorpe's (1951, p. 37) terminology, the birds are in the mood, the preliminary state of readiness for action, necessary to the performance of the instinctive behavior pattern that usually results in both the bird and its releaser-associate arriving at or near a bees' nest. The fact that definite physiological need seems to be unnecessary as a factor in bringing about the guiding behavior suggests that the instinctive behavior involved is, to use a different terminology, what Lorenz has termed an endogeneous stimulus producing phenomenon. In an admittedly loose way, the experiences of many observers recounting their observations from memory, unaided by recorded data, suggest that there may be more guiding in the morning than in the afternoon hours, but this is by no means an invariable experience. It may be that the symbionts are more active early in the day than later on, as the birds have been known to guide humans at all hours, even in the hottest part of the day. As far as I know, in areas where the birds guide frequently, the only times and conditions when the greater honey-guide is known to be unaffected by, or at least unresponsive to, the appearance of a potential symbiont are (1) adult males during the hours of the day when they are established on, and calling from, the call sites or stud posts, and (2) any individuals, regardless of sex, age, or the season, when feeding at a recently opened bees' nest.

Nothing is known of variations in the valence of ratels or baboons under different conditions, but in the case of the human symbiont it seems true that the individual, or group, as the case may be, must be met with in the birds' natural environment. I know of no case where a honey-guide has come into a native village and begun to give its guiding behavior. There are authentic instances of male honey-guides using a tall tree on a street of a sizable town as a temporary call post, but no instance of their guiding in such places. Also, there are authentic instances of their coming into hunters' camps, but these are temporary occupations of otherwise natural environment. Thus, A. Blayney Percival (1924, pp. 347-348) writes that when a honey-guide comes to a camp as it is being pitched, the natives take no notice of it until the chores are done: "They try his patience, for they never hurry; they know the guide will wait. . . . If ignored, he will stay about the camp all day and turn up again next morning." Similarly there are observations of honey-guides attending sizable groups of men on the march. For example, General Bisset (1875, pp. 160–167) relates that while en route with a squadron of cavalry, in addition to an unstated number of infantry, in Natal in 1843, a honey-guide came to them during a halt and guided some of his men to bees' nests.

As far as I have been able to learn, ratels are solitary, nongregarious animals, and I have not heard of more than two being seen together. If, as seems likely, the ratel was the original symbiont, it is of interest to find that the human symbiont is still effective as a releaser of guiding behavior even when in aggregations. Apparently the number of symbionts met with at one time is not of great importance. This would seem to apply to baboons, which are gregarious animals, although in the one described instance of baboon and honey-guide coincidence at a bees' nest, only one out of a small group of the apes was actually involved at the hive.

The imitative actions of the native African human when trying to attract the attention of a honey-guide are apparently designed to increase his potential valence. He grunts in the manner of a ratel and chops on trees to imitate the sound of opening a bees' nest. Since the valence of the symbiont depends on the condition and the "interests" of the honey-guide, it follows that in areas where the species has given up guiding behavior either its needs are satisfied more simply and directly, or else these objects—ratel, baboon, and human, as the case may be—have lost their valence. The two possibilities may be merely different aspects of a single change or they may be separate factors; at present no one can venture to say which. The valance of the objects is judged by their ability to get and to hold the attention of the bird, to elicit from it the needed behavioral response. This does not depend on the responsiveness of the object, although active responsiveness may help to bring out the behavior pattern of the bird. As stated below (p. 59), honey-guides have been recorded as following nonresponding humans for as much as 5 miles without ceasing their "guiding–luring" behavior. We have so little real knowledge of ratels and baboons as symbionts of the honey-guide that we cannot even guess the relative valence of these animals and the African human. We can only treat the three of them together as being similar in this regard, although we should keep in mind Russell's (1935) remarks that "in the case where an animal responds in like manner to a considerable range of objects, which are accordingly equi-valent functionally, it by no means follows that the objects look alike to the animal, or are indistinguishable by it. They are treated alike as having the same or similar functional value, similar valence, but for all that they may be easily distinguishable inter se."

When the African native became aware of the fact that by following a greater honey-guide he would be brought to a source of honey, he quickly improved upon his opportunity by actively and deliberately seeking out the bird rather than passively waiting for it to come his way and lead him. As far as we know, none of the other symbionts of the bird do this, although it should be emphasized that they may well do so. That the bird may regularly take the initiative in such matters is suggested by the case of a honey-guide attempting to attract an unresponsive mongoose to follow it, and also by the very large number of instances in which an unsolicited bird has come to a human and begun to "guide" him. When the bird comes of its own accord to the potential symbiont the only indication we can get of varying strength or intensity of the drive behind its actions is what we can ascertain of its persistence in attempting to get the attention of the would-be follower. Without any critical, even remotely quantitative data, it may be said that at times the bird may be extremely persistent, staying around chattering and flying about for an hour or more, or waiting more quietly for as much as several hours ("most of a day" in some accounts), but immediately becoming alert and active at the first sign of cooperation, while at other times the bird may give up after a few minutes if it fails to get a quick response. There is a similar range of intensity in its response to a native actively seeking it out with his array of grunts, whistles, and stick-knocking. Sometimes the bird will respond by chattering and flying towards him, while at other times it may merely chatter but remain where it is until the native comes to it. This difference in response is not correlated with sex or age or season. Actually, this variability of type of initial response is a general characteristic of appetitive behavior, and may be a reflection of what Thorpe (1951, p. 37) terms the specific action potential of the individual bird. There may even be times when the bird is not interested at all and makes no response, but of these we can, in the nature of things, have no knowledge.

Diminishing frequency of the habit

A clear indication that guiding is not essential to the economy of the greater honey-guide is afforded by numerous and widely scattered observations to the effect that in some areas the bird does not guide, and in others it no longer guides as frequently as it did years ago, and that in some areas it apparently has ceased doing so entirely.

Gill (1945, p. 91) states that near Cape Town, where the bird still is found "chiefly about large farmhouses set in trees (probably always where bees are kept), there seem to be no recorded cases of the bird trying to guide anyone to bees' nests, but cases are frequent enough in natural bush and forest."

According to Rodney Wood (in litt. to J. P. Chapin), the species seldom guides about the southern shores of Lake Nyasa.

Charles Whybrow informs me that during the years he spent in Tanganyika Territory, especially near Malangali (100 miles southwest of Iringa) and Biharamulo (near the southwestern corner of Lake Victoria), he often met with the greater honey-guide, but it never tried to guide him to anything. What is more, none of the natives whom he questioned had ever heard of the birds' guiding habit, which made him conclude that this habit was not so well developed there as in other parts of Africa.

James, of Cradock, Cape Province (in litt. to C. J. Skead), states that in 50 years he has never been guided by a honey-guide. When he was a young man 50 years ago he worked with a farmer who kept bees as a side line, and frequently went with him into the bush to capture wild swarms. Honey-guides often came and sat about while they were working at the bees' nests, but never offered to lead them to any. He further states that his experience as to the absence of any guiding activities by the birds is concurred in by two of his neighbors of long standing.

In response to a query of mine, J. G. Williams, of the Coryndon Museum, Nairobi, writes me that he has talked to a number of observers who have lived in Kenya Colony for many years and that without exception they tell him that the guiding habit of the honey-guide was very much more widespread some 20 to 30 years ago than it is today. In fact, so seldom is it now observed in some places that many of the recent arrivals in the country doubt the whole story and put it down as an old-time hunters' tale! Williams' own extensive field experience confirms this loss of the guiding habit in many places, especially in the vicinity of large towns or in areas where the natives have become more Europeanized in their way of life; good examples are Nairobi, in Kenya Colony, and Kampala, in Uganda. He writes: "In the former locality *Indicator indicator* is a common bird . . . and at Kampala it is fairly frequent, but in neither locality have I ever seen the slightest indication of the guiding habit, and even at Thika, Kenya Colony (a good honey-guide locality), the guiding habit is far from common. It is only when one visits areas where the natives are living under conditions little changed by the whites' way of life that one can be fairly sure of observing the unique association between man and a bird. Eventually, I fear, the habit of guiding will disappear entirely as Africa becomes opened-up and 'civilized.' "

Everywhere I have been in southern and eastern Africa I have made it a point to talk to residents about honey-guides and I was always told that they doubted that the birds guided often enough to get more than a fraction of their food by that means. Furthermore, the fact that other species of *Indicator*, such as *exilis*, *minor*, and *maculatus*, do not guide but still, on autopsy, show beeswax in their gizzards suggests that honey-guides are able to obtain wax without the cooperation of man.

In the more settled and civilized areas where honey-guides have ceased leading natives to bees' nests or, at least, do so less frequently then formerly, this diminution of guiding may be a result of the lesser abundance, if not scarcity or even local extirpation, of the creatures that served to release this behavior in the birds; but it is still more likely that the birds may still lead ratels and baboons and yet be almost never observed doing so. Not only would these symbionts quickly make off into the bush at the advent of a human, but one need only recall how very few actual eye-witness accounts of the honey-guide and ratel association I have been able to gather from areas where guiding still takes place with the native African to realize how improbable it is that such events would be seen and recorded. In the vicinity of Nairobi, for example, baboons are still common although ratels have become scarce, but possibly not as scarce as the paucity of records might suggest. In answer to a query of mine as to whether the natives in that area still make a practice of opening wild bees' nests for the honey they contain, and, if they do, whether honey-guides may not infrequently attend the openings of these hives even though they have not guided the natives to them, Mr. John G. Williams informs me that it is extremely unlikely that any native around Nairobi would go to the trouble of opening up a wild bees' nest. He made extensive inquiries amongst the natives, who replied by asking why should they run the risk of getting badly stung when they can go to the local duka (shop) and buy sugar, or get honey from their own hives. They usually get the honey from their own hives after dark, thereby reducing the chances of being stung by the bees. This has the effect of eliminating this activity from the experience of such strictly diurnal creatures as the honey-guides, which consequently have no occasion to associate the African native with bees' nests.

An unsolicited, corroborative observation comes from Mr. J. Hilton, of the Kenya National Parks, who writes that "one curious note on the honey-guide is that its associations with man only appear to occur in certain areas, usually those frequented by honey hunters. In other areas the bird is present but never tries to attract the attention of man."

After the foregoing discussion had been written, Queeny (1952, p. 396) came to a similar and wholly independent conclusion. He writes that "at one time this unique partnership between man and bird prevailed over the greater part of Africa. . . . But wherever white man encroaches, money is introduced and becomes integrated with the native economy. The natives then earn money-wages. . . . Trading stores spring up, and the natives buy their sweets from Indian merchants instead of securing them from nature. . . . Hence, near Nairobi and wherever white man's ways have become established, *Indicator indicator* finds fewer and fewer natives who will respond to its call. In these areas, generations of co-operation have come to an end and the unique partnership has withered away."

Thus, with the natives' increasing indifference to the birds and the birds' lack of occasion for associating humans with other openers of bees' nests, it is understandable that guiding might lessen or even cease. The important point, and on this we have no information, is whether in these areas the other mammalian symbionts still cooperate with the honey-guides.

However, it does seem that in the more civilized regions the ratels have become either very scarce or almost wholly nocturnal (which amounts to about the same as far as a diurnal creature like *Indicator indicator* is concerned) and the baboons have decreased greatly in numbers. Furthermore, in such areas, relatively few of the natives, compared with those in "unspoiled," unsettled areas, have the free time or the inclination to follow the birds to bees' nests. The potential valence of the human as a symbiont has decreased too greatly for the bird to react to it in these areas.[10]

That the greater honey-guide does not attempt to "lead" humans in areas where it has had no opportunity to connect them with bees' nests suggests that, in areas where it does, it has to learn to recognize humans as potential symbionts and that it has no innate tendency to do so regardless of prior experience. This seems to be essentially similar to what transpires in the learning processes of other, quite unrelated birds. For example, Sumner (1934) found that the young of some western North American raptorial birds do not reveal any inherited ability to recognize living animals as prey, but have to learn to do so. It would seem that the honey-guides probably have an inherited tendency to be interested in bees' nests, as they consistently reveal this with no possible experience of parental action as a model, being reared, as they are, by a variety of hosts devoid of any such habit, and being essentially nongregarious after leaving their foster parents. It would also seem that they probably have an innate tendency to remember and to recognize the creatures they find foraging at bees' nests. Beyond this, we need only to recall, as Nice (1943, p. 64) points out in her study of passerine behavior, that an animal "has to deal with man according to its store of instinctive actions. An animal knows parents and other members of the species. . . . Otherwise the animal knows enemies, and animals to which it is indifferent."

In a recent analysis of social cooperation in animals, Tinbergen (1953, p. 85) concludes that, so far as present knowledge permits a generalization, this cooperation seems to depend largely on a system of conspicuous but relatively simple releasers, and that while the tendency of the acting animal to give these signals is innate, as are also the responses of the reactor individual, the picture becomes complicated at times. This is due to the fact that "many social animals respond to the species' social releasers only when provided by certain individuals, which they know personally. In such cases personal connexions, established through learning processes, confine the reactor's responses to signals from one or a few individuals only." If this may happen with such deeply innate behavior releasers as intraspecific ones, it is not surprising to find it happening more readily with relatively more recent and more superficial interspecific ones of the sort we have been discussing between the honey-guide and the human.

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[10] It may be that the mechanism here is not too dissimilar from that operating, in a different direction, in protected areas to make the human less fear-inspiring and less an object from which to flee. Thus, nighthawks (*Chordeiles minor*) nesting on gravel-covered roofs of buildings are said to indulge in injury-feigning reactions considerably less than do terrestrial birds away from towns. The relative absence of shyness in ducks in protected areas or after the close of the hunting season seems to be another similar change.

Behavioristic level of the habit

Use of the term "guiding," with respect to the behavior pattern that usually results in the follower arriving at a bees' nest, is unfortunate in that it implies a preexisting purpose or plan on the part of the bird, an intelligent activity far beyond the psychological capacity of any bird. We must distinguish at the outset the difference between the purely instinctive behavior of the individual "guiding" bird and the biological end or survival value of this activity. While we have no reason for assuming that the individual bird has any "purpose" or "plan" when it "guides," which is an unthinking act on its part, it still is true, in an evolutionary sense, that the species to which it belongs has developed a guiding habit. It is only of the species as a whole, viewed over the ages of its existence and development, that we may speak of a purpose or goal behind its behavior, and to impute this to the individual members going through a purely instinctive behavior pattern is not only unwarranted but misleading and philosophically dangerous. The word "guiding" has a purposive connotation which is applicable to the species but not to any of its members.

Aside from the fact that we cannot assume any intelligent plan on the part of the bird, there are several features of "guiding" which further indicate its stereotyped nature. One is the fact that guiding ordinarily is not direct. The bird frequently leads in a most erratic course, often actually going a considerable distance beyond a bees' nest and then coming back to it. I have estimated on four different guiding experiences that the time and distance involved varied from 50 to 130 percent greater than if the bird had led in a direct path to the bees' nest. The diagrams of guiding routes (fig. 5) are all from places where there were no barriers to be gone around, and where trees were numerous and fairly evenly spaced. In other words, in none of these cases were the paths determined by directly observable limiting conditions.

If guiding were purposive in the individual this would be difficult indeed to explain, especially since there were no obstacles or barriers such as hills, ravines, etc., to be by-passed. On one of these occasions I was led for 21 minutes over a distance of about 750 yards; on returning from the bees' nest to the starting point, I found it took only 9 minutes walking at the same rate, and that the distance was only about 350 yards. On another guiding trip lasting 12 minutes and involving a distance of 350 yards, the return without the bird took a

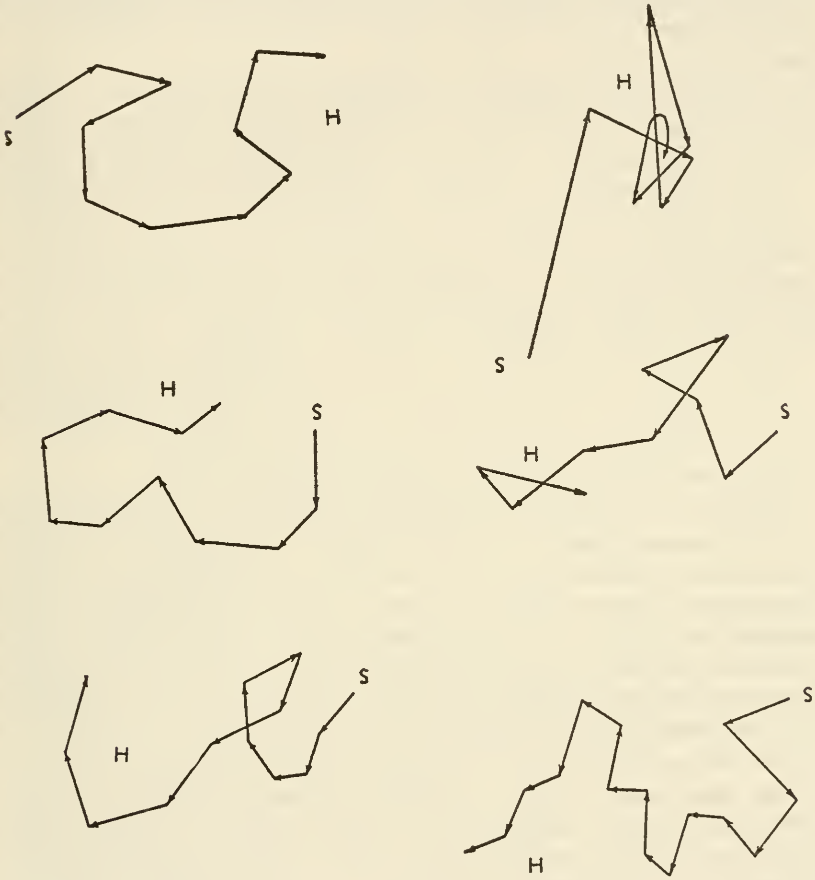

Figure 5.—Diagrams of routes taken by guiding birds. The figure in the lower left corner is taken from Skead (Ostrich, vol. 17, 1946, p. 200), the others are from the author's own experiences in Zululand and Natal. In all cases the breaks in direction are at trees where the bird perched waiting for the follower. In each the letter S is the point at which the trip started and the letter H the location of the beehive to which the bird led.

little under 8 minutes and the distance was about 250 yards. I may say that all my guiding tours were timed by watch and measured by actually counting the paces between the trees on which the guide rested between flights and by assuming an average of about 2 feet per pace through the bush. Even if there may have been an error in the absolute measurements, the relative distances of the guiding course and the direct return are fairly accurate as both were measured in the same way.

A lesser point is the fact that the guide is actually out of sight of the follower most of the time, the guiding depending largely on the bird's chatter, and, of course, also on its conspicuous dipping flight as it goes from one tree to another with its white outer tail feathers widely spread. To a ratel or a baboon this matter of following a sound rather than a sight may make little or no difference, but the way in which the bird acts while guiding is quite similar to that of a bird that is trying to get away from one, even though it does wait at its next resting spot until the follower comes near. All naturalists who have tried to follow birds to see them better have had the experience of getting fairly close only to have the bird fly off to another tree 20–50 yards away, and then have to start following it over again. This is essentially what happens during a guiding tour.

While the actual behavior involved in guiding is not too dissimilar to diversionary display, it is accompanied by the all-important factor of the bird seeking out, of its own volition, the object of its display. Armstrong's terms "delotropy" and "delophony" could readily be applied to guiding. The delophonic aspect of this behavior, coupled with the fact that the guide is actually out of sight of the follower so much of the time, raises a point of possible phylogenetic significance. The species of *Indicator* nearest to the original stock, *I. maculatus* of West Africa, is not known to guide, but the natives in the Cameroons claim that its call *woé woé* means "honey-honey," and that they sometimes go to such a calling bird and find a bees' nest nearby (Bates, 1909a, pp. 15–16). As Bates puts it, the natives know nothing about following this bird, and that would be an extremely difficult thing even for a native to do in the forest. This makes one wonder if guiding in its incipient stages, especially in a bird of the dense forest, might not have been more a matter of sound than of sight. This further suggests that the preponderantly delophonic nature of the guiding behavior in *I. indicator* may be, to some extent, a survival from, and a reflection of, some such ancestral pattern.

Still another bit of evidence as to the nature of the performance is the fact that on occasions the bird will lead not to a bees' nest but to a dead animal or to a live snake, leopard, rhinoceros, etc. I doubt that these are in any sense the "purposive" goals behind the species' habit of guiding, and that in most cases they may be dismissed quite easily as distracting incidents on the guiding trip that cause the guide and, more certainly, the follower to "forget" the original "goal." Such cases are much more frequent in the literature than in reality, as they make exciting traveler's tales, but they do happen. Many years ago David Livingstone tried to ascertain the truth of such tales and actually asked 114 of his natives if they had ever been guided by a honey-guide to anything but a bees' nest. Only one out of the 114 could recall that he had had such an experience although all had been guided on a great many occasions. Percival (1924, pp. 347–348) reports essentially the same on the basis of his natives' experience. Blancou (1933, p. 317) considers it purely a matter of chance or accident if the bird happens to appear to "lead" to a large animal.

A little over a century ago the French naturalist Delegorgue felt, from his observations in South Africa, that when a honey-guide led to a dead animal it seemed to be interested in feeding on the flies and maggots on it. More recently, in Portuguese East Africa, Vasse corroborated this in the case of a dead buffalo to which he had been led by a honey-guide.[11]

Major Haydock, in Northern Rhodesia, was told by his native collectors that when a honey-guide led them to a leopard or a lion it was always a sleeping beast, and that the bird seemed to mistake the flies hovering about it for bees (this is the natives' own, unaided conclusion). It seems very probable that the real explanation is that the flies hovering about may have a similar effect on the honey-guide as would a flight of bees. In some of these instances the observers made particular search to see if there might have been a bees' nest near the animal; if so, the animal's presence could not be looked upon as more than a coincidence, but in a number of cases there was no sign of a hive.

It might be mentioned, parenthetically, that there are some who think that the actions of the bird may be slightly different when coming to a large animal than when arriving at a bees' nest. So few detailed data are available that it is not possible to say what the exact points of difference are, but the following incident suggests that to the eyes of observant natives there may be some subtle revealing variations in the behavior of the honey-guide. Mr. John Sim, game warden at Kapenguria, western Kenya Colony, informs me (in litt.) that once he was hunting in thick bush in the Suk district when a honey-guide appeared, fluttered around, and then descended several yards away into the dense undergrowth surrounding the path. One of his Suk guides immediately stopped and said, "When that bird alights, there will be dangerous game." He spoke with such conviction that Sim was impressed, and proceeded slowly to the spot, and there found a rhino lying down. To quote from Sim's letter:

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[11] It may be mentioned that this suggestion has been amplified in an unwarranted fashion by Gromier (1949, pp. 168–169), who attempted to explain his being led by a honey-guide to a buffalo by suggesting that the bird knows the hunter will kill the buffalo and then carrion flies will lay their eggs in the carcass and later the eggs will hatch into maggots, on which the bird likes to feed!

> In case the point should arise, I am prepared to say definitely that the bird was a honey-guide and not a tick bird. What the bird's intentions were must be a matter of conjecture . . . Unfortunately I did not ask the Suk why he was so convinced that the bird wished to lead us to dangerous game and not its normal objective of a bees' nest . . . The incident took place about three years ago. Any attempt to discuss the matter met with a silence so significant that I abandoned the effort. Since, now discussion has been invited, I offer with fear and trembling the above highly improbable, quite inexplicable, but perfectly true account of what happened.

It is also to be kept in mind that occasionally bees and dangerous animals may be met with simultaneously with the result that the latter are recalled more vividly than the former. Two such instances, related by Mr. D. Tolnay of Marandellas, Southern Rhodesia, are as follows. Once, near Palape Road, he followed a honey-guide to an enormous termite mound where he found a bees' nest. As he was looking at the bees buzzing about the crevice that led to their hive, a banded cobra came out of another hole in the same mound. On another occasion, in Natal, his father followed a honey-guide to a small cave. He saw bees in the immediate vicinity and some coming out of the cave as well. He entered the dark recess and found some bee comb in a crevice. When he made a fire to smoke out the bees, he was startled when a leopard rushed out past him to escape the smoke. Either of these cases might easily have been written up as evidence of the bird leading to dangerous animals, whereas in both cases there were bees present.

I need hardly add that I have discarded the great majority of recorded tales of honey-guides leading to large animals because they were not free of suspicion, either on the grounds of incomplete observation (such as the possibility of the nearby presence of unseen bees) or because of loose writing. Even in the case related by Mr. Sim there is the possibility that the Suk guide was repeating a legend which appeared to ring true because of a fortuitous circumstance. If there had been no rhino there, Sim would probably have thought his guide's words were just another naive belief of the natives, and would probably have forgotten the whole incident, but the definiteness of the pronunciation, bolstered by a very few other similar instances, makes me feel it wiser to keep an open mind on the subject, doubtful though it seems.

If the guiding bird had any such thing as a prearranged plan, it would be almost necessary to assume that it would guide to a previously selected bees' nest, or at least to one of a group of known bees' nests. That "guiding" may lead to bees' nests that could not have been previously selected by or even known to the bird is evidenced by the following experience communicated to me by Captain Davison of the Wankie Game Reserve in Southern Rhodesia. He had a group of his natives at one of the rest camps in the Reserve when a honey-guide came to them and chattered and went through all the motions of trying to get them to follow it. Davison refused to let any of his boys go, but got them all on a truck and drove off to the next camp some 5 miles away. The bird followed them all the way and then Davison told one of the natives to get an axe and follow the bird. The honey-guide "led" this native to a bees' nest less than half a mile from the second camp, but which must have been at least 4½ miles from where the bird first began calling to them. Certainly 4½ miles is many times farther than any honey-guide has ever been known to "lead" a follower, and it is highly improbable that the bird even knew of this bees' nest. Davison felt convinced that it was the same individual bird throughout this observation.

While much is still to be learned, the following brief description seems to summarize our present understanding of the guiding habit. The releasers of the instinctive behavior constituting "guiding" are the sight or sound of ratels, baboons, and humans (away from villages). The stimulus which apparently brings these actions to a halt is the sight or sound of bees. It is tempting to expand von Uexküll's and Lorenz's fruitful concept of the "kumpan," or companion, as the releaser of instinctive actions in birds and apply it to the honey-guides. The three animals known to be "guided" to bees' nests by the birds are creatures the birds probably have ample opportunity of associating with bees' nests because all three (ratel, baboon, and human) break open bees' nests regularly. At times, when they are doing so a honey-guide appears on the scene, possibly attracted by the sound, but also because honey-guides are often given to perching near places where bees swarm. In such cases there is no "guiding" behavior, probably because the sight or sound of the bees flying about is sufficient to stop such behavior patterns from being released by the otherwise releasing "kumpan." From this standpoint guiding may be looked upon as the result of the reactions evoked in the bird when the releasing agent is met with in the bird's natural environment, away from the bees' nest, for which it is the "kumpan," and the "guiding" behavior is "satisfied" or, at least, brought to a stop when the bird brings together the "bee companion" and the bees.

At this point it seems worth while to interpolate a suggestion for future work on the nature of the bond between the bird and its foraging symbiont. If the bird is subjected to an experience even slightly similar to what, in Lorenz's terminology, would be called "imprinting" by association at a bees' nest with the African human, this "imprinting," if such it be, might more likely occur with young honey-guides than with old ones. In areas where humans no longer open wild bees' nests and where honey-guides make no attempt to "guide" them, it might be instructive for resident naturalists to deliberately open a number of such wild hives and see if this might stimulate the birds to react towards humans with what we have come to consider "guiding" behavior. It would be interesting to see if such induced results would be more pronounced in immature (yellow-throated) than in adult birds. We have no data as to how soon after leaving the care of their foster parents the young honey-guides begin to "guide"; we only know that birds in immature plumage guide frequently, and that this plumage is not completely replaced until the second year of the bird's life.

Further evidence to the effect that it is the sight or sound of bees and not any previous knowledge of a particular hive that brings to a halt the "guiding" of the birds is the following item related to me by C. J. Skead (in litt.). He was informed that two locally well known bird observers, F. G. Turberville and his son, once followed the guiding chatter of a greater honey-guide and were brought not to a bees' nest but to a small, heavily flowered, sweet-scented shrub about which bees were swarming and feeding on the flowers. A careful search failed to reveal any sign of a hive nearby.

Another observation illustrating the nonintelligent nature of guiding was related to me by Skead (in litt.). He knew of an exposed bees' nest on his farm for many years. The comb hung there in plain view, within easy access through an opening 9 inches wide. If ever there was a bees' nest available to the honey-guides without the need of human intervention this was one, and yet Skead was guided to it by a honey-guide on one occasion.

Still another point may be made. Honey-guides have never been reported to lead to long-deserted bees' nests even though they might be full of comb. They seem to require the sight or sound of the bees. They have been known to lead to new and as yet quite empty bees' nests, merely attracted by the flying insects.

It might be argued that in those cases in which the same bird has been known to lead a person to more than one bees' nest in succession would indicate that the sight or sound of the bees did not serve to bring the guiding behavior to a stop. However, in these cases there seems always to have been a definite break, or cessation, of the guiding at each of the bees' nests. It appears that it was only after the follower showed no interest in the bees' nest that the bird edged off and then, as the person came near it, began to "lead" again.

It must also be remembered that just as the ratel or baboon or primitive human may be the "bee kumpans" to the bird, so the honey-guide may be equally the "bee kumpan" to the ratel, baboon, or primitive human. In our wonderment at the "strange" guiding habit of the bird we have generally forgotten to consider the equally remarkable "following" habit of these mammals. We must remember that the "following" is voluntary; the mammal does not have to follow the bird, and, in the case of the ratel, both the guide and the follower mutually stimulate each other by sound throughout the trip, the end of which is apparently often, if not usually, unknown to both when they start out. In the case of the primitive human the noises made by the follower are imitations of the call of the ratel and of the noise made by chopping open bees' nests, obviously designed to heighten the associative significance of the human follower to the bird. That the grunting call given by the South African natives is such a direct imitation is evidenced by the incident related previously about the Zulu game guard who said that a ratel sounded "just like a native calling to a honey-guide."

The behavior of the honey-guide on coming to the vicinity of a bees' nest is of interest in this connection as it throws some light on the nature of the guiding habit. Inasmuch as we are still in the stage of groping for clues as to the original nature of the habit, we can ill afford to neglect any bit of evidence, slight as it may be. In order to avoid placing undue value on such evidence, we may begin by stressing its great variability. In almost every case in my own experience (22 out of 23 guiding trips) the bird became and remained silent when at or near the bees' nest at the end of a noisy guiding trip with all its usual accompaniment of constant chattering and successive flights. Other naturalists have had quite different experiences, as will be pointed out, but the fact that the bird frequently suddenly becomes silent and perches quietly in a convenient tree nearby is not without significance. If the immediate (as contrasted with the biological) end served by the guiding habit were merely the opening of the bees' nest and the getting of the food from it, one might plausibly expect the tension and excitement of the bird to increase noticeably when it arrives at the hive. Yet, what often transpires is just the opposite. All the bird's activities and movements subside and it remains unobtrusively in a nearby tree. Whatever activated it before has suddenly been "satisfied," and the only observable thing that has happened is that the bird has been exposed to the sight and sound of flying bees. In two cases of personal observation, after reaching the bees' nest we had to send a native back to camp for an ax and a spade, and we merely sat there until his return. In one of these instances this took over three-quarters of an hour, in the other about an hour, but, in both, the bird that had led us there with constant chattering and successive flights remained silent and motionless nearby. It actually stayed that way for about an hour more while the natives chopped open and ransacked the hives. Several "old-timers" with whom I have talked in Africa and numerous writers have also found the birds to remain silent about the bees' nest, which gives me reason to think my observations were not atypical.

However, as intimated above, there are many exceptions to this in the observations, published and unpublished, of others. Thus, in the instance (described in our account of the mammalian symbionts of the guiding bird) when Major Beaton found a honey-guide associated with two ratels demolishing a hive, he was first attracted by the bird's chattering. He found the bird perched well up in a tree directly over the hive, chattering loudly as the ratels worked away beneath it. Skead (1946) recounts an occasion when he was unable at first to find the bees' nest when a honey-guide led him to it and writes: "After I had been searching for about a quarter of an hour the Honey-guide called less and less and eventually gave up altogether and I did not see it again." This implies that the bird was not silent at first in the vicinity of the bees' nest. In a later paper Skead (1951, p. 58) writes that usually on arriving at a hive, the bird perches above it or to one side of it, "calling as before."

Many years ago at Mariba's Hoek, in the northern Transvaal, the late Austin Roberts and I had what was superficially a somewhat similar experience. We had followed a greater honey-guide through the bush when it made a last short flight to a tree and then stopped chattering and sat erect. We made no move, and in about a minute or two the bird flew around us chattering noisily and then went back to the same tree and again stopped calling. We were unable to find any sign of bees there, but it is probable that there was a nest nearby which we failed to notice. This case raises the possibility that the chattering of the bird at the hive vicinity may be something induced to some extent by the lack of response on the part of the follower. The fact that Skead never made any attempt to open a bees' nest when led to one leaves his observations in more or less the same category; at least they do not settle the possibility. This, however, could hardly be said to apply to the Beaton case, and apparently is equally inapplicable to the following observations by Jackson (1938, pp. 731–733). Sir Frederick was out hunting with an old Andorobo when a honey-guide began to "guide" them. "After going about half a mile the bird flew on to a small thorn tree growing on the very brink of the quarry, and became more noisy and excited than ever, and on looking over the edge, sure enough there were the bees going in and out of a small crack. . . . On a previous occasion . . . we first heard and then saw a Honey-Guide, and the Anderobo at once went off in pursuit. . . . After a break-back struggle through, under and over the dense tangled undergrowth, we came up with the bird in great exitement, sitting on the dead branch of a Podocarpus tree, and there was the bees' nest in a small hole about thirty feet from the ground."

It appears that while these cases do not seem to fit in too readily with the thought suggested above, the discrepancies are not insurmountable. We do not have sufficient data on any one of these cases to attempt to "explain away" the variation in pattern it presents, but it does not seem unreasonable to suggest that any activity of so complex a nature as guiding is open to the influence of many factors and that therefore a lack of rigid uniformity in its expression is not necessarily a negation of its underlying pattern.

Inasmuch as the honey-guides catch and consume quantities of insects, the question arises as to why they should be especially interested in bees' nests. It is now possible to state that the thing of primary concern to them there is not bee larvae or honey but beeswax, and this item is, of course, the one thing they cannot get elsewhere. We still do not know just how essential beeswax is to the birds, but it is evident that they not only eat it regularly and avidly and extract nourishment from it but when given the choice between plain, dry wax and comb full of honey and larvae they prefer the dry wax. In this they are unique among birds, and it is this wax-eating habit that must have preceded and framed the development of the so-called guiding behavior. However, inasmuch as the birds can get wax without guiding, as do the nonguiding species, it follows that the origin of the guiding habit was not necessitated, but merely expedited, by the antecedent cerophagous tendencies of the birds. It should be recalled that the birds seek out the creatures which, by releasing the "guiding" behavior, become the followers, and that, as Lorenz pointed out, instinctive actions differ from mere reflex actions in that the former are "desired reflex actions." Being sought or desired is the one point in which instinctive actions differ from all other reflex actions. Since guiding is not essential for food-getting, and since honey-guides show very little tendency to indulge in courtship display, the possibility that the basis of guiding behavior may be a displaced display activity cannot be ruled out without due consideration. Cases of displacement of behavior patterns from their apparently original loci to quite other areas are not unknown; in the present instance this displacement, if such it be, is remarkably wide and permits individuals of both sexes, immature as well as adult, to take part. Whether we look upon guiding as a form of displaced courtship display or not (and I think it is doubtful), the actions involved in it lead us to ask, as von Uexküll (1909) did, how drives and motives are related. What we seem to have here is something akin to a nonpurposive pattern extending over into one that superficially gives the appearance of having an anticipated purpose or usefulness.

Antiquity of the habit

A habit that depends for its expression on the cooperation of two totally independent animals cannot have developed suddenly, or recently, as some writers have suggested. These writers were probably misled by thinking that guiding was primarily a matter of leading humans, and that, therefore, the habit could not be older than the presence of humans. As we now know, this is not the case, and, as we shall see, guiding is probably an old, and, in an evolutionary sense, a residual habit, and like many relicts is neither essential to the species that have it nor productive of any descendant differentiation.

We may recall, at the risk of repetition, that of all the honey-guides only one group, and that a relatively "primitive" one (at least the one least differentiated from the hypothecated ancestral stock), developed the guiding habit, although all but *Prodotiscus* feed on bee comb, and all of these would have opportunities to meet with foraging mammalian or other associates at bees' nests. We know definitely, from direct observations, that an apparently nonguiding species, *Indicator minor*, sometimes comes to a bees' nest as it is being opened by natives who were led to it by a greater honey-guide, and that it feeds on the bits of comb together with the bird that did the guiding. As already intimated, it cannot be said that the lesser honey-guides, or some others of these species, do not have any guiding tendencies merely because they do not make any attempt to lead humans, but in the case of so well known a species as *I. minor* we would probably have had some observational evidence by now if it did associate itself with any other creature in its raids on bee comb. In the literature one often finds the statement that the honey-guides are poorly equipped to open bees' nests unaided, and this is supposed to help account for their having assumed a symbiotic relationship with animals more able to tear open these food sources. Yet, of all the honey-guides, the ones that have entered into such mutual forays on the bees are among the very species with the largest, most powerful bills. The evolutionary trends in the honey-guides have produced two lines characterized by reduction in bill size, one leading to the subgenera *Melignothes* and *Pseudofringilla* and the other to *Melignomon* and *Prodotiscus*. One line has retained the large bill, the subgenus *Indicator* and its specialized offshoot, *Melichneutes*. The subgenus *Melignothes*, as illustrated by *I. minor*, its best known species, is more of a flycatcher in its feeding habits than is *I. indicator*, although the latter also catches some of its insect food in that manner. While *Melignothes* and *Pseudofringilla* and *Melignomon* all still eat wax regularly, it seems likely that their evolutionary trend is in the direction of less dependence on bee comb as a primary food source. This condition has actually come to pass in the case of *Prodotiscus*, the end result of the *Melignomon* line, to the extent that neither of its included species any longer eats bee comb and its various inclusions but feeds on scale insects very largely. This, in turn, suggests that the primordial honey-guide stock may have been differentiated early by its wax-eating proclivities from the line that produced the barbets. This, again, has the theoretical advantage of providing an antiquity for the wax-eating habit sufficiently great to have allowed for the development of so complex a behavior pattern as guiding, a habit which is obviously based on, or at least developed within the limits set up by, an antecedent cerophagous tendency.

If the basic honey-guide stock attempted to open hives, as seems not improbable (and they are the one section of the family even partly able to do so), they might have developed a symbiotic relationship with other bee predators (ratel, baboon, etc.), while the other groups of the family with still poorer hive-opening equipment (smaller, weaker bills) seldom or never made any such attempt themselves but were merely involved, in an opportunistic sense, in the results of these predator's raids. In other words, they were, if anything, followers and not guiders—and followers only in the loose sense that jackals and vultures are followers of carnivorous predators such as lions and leopards. This seems to be reflected in the apparent absence of guiding in these species of honey-guides. Thus, it seems not unlikely that once the evolutionary trends towards less dependence on bee comb and reduction in bill size set in, in the past history of the Indicatoridae, there was no further incentive for an evolutionary dispersal of the guiding habit into the then newer, formative groups. It would appear, then, that guiding is not a recent development in the honey-guides but an old, yet sharply restricted trait confined to a single branch of the family.

That the honey-guide, or, more specifically, the greater honey-guide, had a prehuman associate in its guiding behavior has now been demonstrated beyond doubt. This was an important point to establish, and it was for this reason that I went to so much effort to gather evidence on the ratel and other possible collaborators of the guiding bird and to record these data in detail. And yet, even with these prehuman associates, guiding apparently was never the sole or even the basic method of food-getting either for the bird or for its symbionts. The fact that many species of honey-guides do not guide (as far as known) and yet get enough wax regularly (practically all specimens collected have had wax in their gizzards) shows that guiding is not necessary. That it probably never was essential seems to be reflected in the fact that it did not "carry over" into the other phylogenetic branches of the family.

Evolution of the habit

Reference to our discussion of the phylogeny of the species of Indicatoridae will show that the guiding habit is restricted, as far as we know, to one branch of the family, that comprising part of the subgenus *Indicator*, including *I. variegatus* and *I. indicator*. We still have no data as to guiding in a third related species, *I. archipelagicus*, which, on phylogenetic grounds, might conceivably be expected to reveal some signs of such behavior. There is, unfortunately, a similar lack of knowledge of the habits of the species supposedly nearest to the progenitor of the whole line, *I. maculatus*, but in that species there appears to be less reason to expect guiding, unless in a very incipient form, than there is in *I. archipelagicus*. Enough is known of the habits of *I. minor* to be able to say that it does not guide humans, and the same seems to be the case for its smaller relative, *I. exilis*, while our knowledge of the species of *Prodotiscus* makes it clear that they do not possess any guiding tendencies and do not even feed on bee comb. In a specialized derivative from the typical *Indicator* stock, *Melichneutes robustus*, guiding is still to be demonstrated. The aerial evolutions of this bird can hardly be connected with guiding behavior, as they "lead" to nothing but empty sky, and when the bird does finally descend into a tree it is after a course that no nonvolant creature could possibly have followed. These aerial gyrations would seem more probably to be a matter of courtship activity, but their real nature remains to be discovered.

Although guiding behavior is known for only two species of *Indicator*, we do know that all the honey-guides except *Prodotiscus* eat beeswax. From the admittedly meager accounts of their habits and from the trapping of several species in the West African forests, we know that other species (*I. maculatus*, *I. exilis*, and *M. robustus*) come to places occupied by wild bees to peck at any wax they can reach. This is also true of *I. archipelagicus* and *I. xanthonotus* in Asia. As may be seen in our discussion of their feeding habits, *I. indicator*, *I. variegatus*, and *I. minor* can and do get wax from accessible wild bees' nests at times by themselves, but it is true that many and possibly most of these sources are not readily available to them until opened by some other bee predator. In this way the birds come in contact with other creatures attracted by honeycomb, some of which are better equipped and more able to open these hives and make accessible their contents.

Then the honey-guides get a share of the wax from the leavings of their abler predatory associates. In this way, to put the matter briefly and crudely (and we do not have the data with which to express it more accurately), these animals become familiar and important to the birds.

As pointed out to me by Chapin (in litt.), in a somewhat similar way monkeys seem to have become important to hornbills of the genus *Tropicranus* because they scare out large insects; similarly, large grazing mammals became attractive to cattle egrets (*Bubulcus*), cowbirds (*Molothrus*), and flycatchers (*Machetornis*) because they flush grasshoppers and other insects, and they became attractive to oxpeckers (*Buphagus*) because they carry ticks.[12] In these cases the birds do not deliberately attract men to their large mammalian comrades. There is, of course, no reason why they should, for men would not thereby increase their food supply. The fact that in *I. indicator* and *I. variegatus* the birds do "lead" humans bears out the contention that to these birds a potential foraging symbiont is merely any creature associated from previous experience (?) with the opening of bees' nests, and is therefore only an extension of the ratel-guiding association. The human element has served to bring the habit forcibly to the attention of naturalists, but is, in itself, of lesser interest than the basic symbiotic tendency of which it is a partial displacement.

The displacement of a wild mammal by a human in part of the life of a bird is not peculiar to honey-guides. A roughly analogous case has been reported for the European robin, *Erithacus rubecula*, by Geyr von Schweppenberg (1951). He writes that this bird appears to have a tendency to come to a large animal—horse, deer, badger, or bear—and even to a man working in the woods; the apparent reason for this trait being that the robin thereby obtains insects scared up incidentally by the mammal's activities. That this tendency in the robin is innate rather than learned is suggested by its short life-span and solitary habits. It would seem that this feeding habit may well be older than the possible association with humans; in other words, that it started with grazing quadrupeds and later was extended to include humans in similar situations. We know nothing of the longevity of honey-guides, but they do parallel the case of the robin in that they are rather solitary, and in that they will come to humans out in the bush but not to men in native villages or compounds.

While not of the same degree of pertinence, it may not be out of place to recall that in his general, philosphical discussion of the roles of the various "companions" as releasers of behavior, Lorenz (1935) finds that the pattern of the social companion is generally poor in inborn characteristics, so that a great deal of latitude is given to the imprinting of the object chosen. He writes that he did not know of a single kind of bird with well developed social tendencies whose social instincts could not be molded upon the human being.

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[12] Rand (1954) has recently brought together many types of feeding relationships.

The human element has also tended to cloud the possibility that guiding may occur in some of the species of honey-guides which do not extend this habit to include human associates but may restrict it to some mammalian or other forest denizen rarely, if ever, observed in this capacity by human eyes. Of this we know nothing, and, of course, it may have no existence in reality, but we cannot dismiss it summarily for lack of evidence.

But, if the honey-guides, as they roam about through the bush, were to see one of the creatures they associated with when feeding previously at some time at bees' nests, they might become "excited" and noisy. That would furnish a possible starting point for "guiding" to bees' nests. It is necessary to digress for a moment to discuss briefly the difference between mere "excitement" and its possibly induced vocalisms on the one hand and guiding behavior on the other. Helmet-shrikes of the genera *Sigmodus* and *Prionops* are frequently reported by natives to "scold" loudly when they see a leopard, thus serving, inadvertently, to attract the attention of any passing human being. In the Cameroon forest there are squirrels which give a special call when they come across a large snake, and the native hunters know this call and make use of it to help in their search for the snake. The squirrel gains little by this behavior and does not really lead men to the snake. Furthermore, it appears likely that this special call would be given regardless of the presence or absence of a human nearby. But there is no reason to think that the honey-guides react to bees as to enemies,[13] but rather that such reaction is an indication of the presence of wax which they want to eat.

The animals that the honey-guides meet with at the bee trees are ordinarily intent only on opening the bees' nests and eating the contents, and are, therefore, not frightening to the birds, which merely wait quitely nearby for their turn to come down and feed on the scraps left strewn about. It appears that the birds come to associate the sight of these foragers with bees' nests and subsequently the sight of any of them, when encountered elsewhere, may evoke in the birds an apparently excited vocal response. That it really is something akin to associative memory is suggested by the fact that in areas where native humans no longer open wild bees' nests (but rely for sweets on trading stores or on domestic hives) and no longer go about in the bush calling to honey-guides, the birds no longer make any attempt to lead men to bees' nests. They simply do not have the experience of associating humans with bees, and hence there is nothing on which to base or develop the associative memory necessary to cause them to make any attempts to guide humans.[14] Conversely, in those areas where they do still gather wild honey, the natives, in trying to enlist the help of honey-guides, use methods which make use of associative memory on the birds' part by imitating the grunts of the ratel and by hitting on trees to imitate the sound of chopping open bees' nests.

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[13] It is true that Hoesch (1937) tried to interpret guiding as an attempt on the part of the birds to lead associates to destroy their mutual "enemies," the bees, but this cannot be taken seriously.

Inasmuch as the present discussion involves memory on the birds' part, it should be mentioned that Thorpe (1951, pp. 277–278) has brought together data showing that some birds may remember individuals for over a year. He emphasizes that "where the learning concerns types of food available only at a certain time of the year, of situations linked with a particular phase of the breeding cycle, a memory of less than 12 months' duration might be of very little biological advantage." Associative memory is thus highly probable.

However, while the above-mentioned imitative acts of the natives serve to increase their chances of enlisting the aid of the birds, they are not necessary, as frequently the birds come to men unsolicited and then begin their guiding behavior. Allowing for the probability of associative memory causing a proper response, we still have to account for the birds beginning to entice their "followers" to a distant place where bees are swarming. To assume that the honey-guides chattered at their bees' nest associates at greater and greater distances from the focus of feeding interest is in itself not a very great assumption, and it would be about all that is needed. There is no reason for assuming any rationalizing on the part of the birds, but to credit them with the ability to recognize "useful" animals, such as ratels and humans, is not too hazardous. Experiments have shown that many birds distinguish predatory hawks from other large birds by their silhouettes against the sky. Chapin points out to me that *Buphagus* obviously distinguishes between various large mammals for it is attracted mainly by rhinos, hippos, buffaloes, giraffes, large antelopes, and wart hogs but relatively seldom by elephants, zebras, wildbeest, and small antelopes.

It requires no great assumptions to see how the honey-guide and the ratel or other bee-predator originally came in contact with each other. What does still pose a question is how did the bird come to begin to "lead" the ratel instead of merely chattering at it when the two happened to meet away from a bees' nest. In the case of the relatively "primitive" spotted honey-guide, *Indicator maculatus*, the bird is said to call (at times, at least) from the vicinity of a hive, but it is not known if it calls to anything; it may be no noisier there than it is elsewhere, and, as far as our very limited information goes, its note may be no different when near a bees' nest or far from one. Detailed observations on this honey-guide are sorely needed. Unfortunately, information on the guiding habit in the next species in the phylogeny of the group, *I. variegatus*, is also very meager, but the little we have suggests no behavior notably different from that of *I. indicator*. It would seem, and this is admittedly speculative, that originally the bird probably knew of one or more bees' nests, and when coming upon a ratel began to chatter as if in anticipation of the latter being already at the hive (with which the creature was associated in the bird's memory), and flew back to the known hive, followed by the *Mellivora*. The flight back to the known bees' nest might have had to be a repetitive affair until the slower moving mammal reached the spot. From this it seems there developed the tendency to chatter to a symbiont even when no particular bees' nest may have been close at hand, and that the resulting series of flights that we call guiding eventually halted when the bird saw or heard bees flying about. Thus, originally, "guiding" would seem to have been more accurately a matter of leading to a known goal than it has since come to be. That it was never essential to either the bird or the mammal permitted its development as a habit in both as a more or less adventitious addition to their regular food-seeking activities, and it may well have assumed a greater and greater role in time. It is, however, difficult if not impossible to imagine the development of such a habit if it were the chief foraging method, as it would have been of no conceivable value to either until it was perfected by both.

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[14] One may recall that in her discussion of conditioned actions, Nice (1943, p. 60) concluded that the "activity is innate but its object is often learned," agreeing with a similar conclusion reached by Lorenz (1935).

To summarize: The bird evinces an excitement type of behavior when meeting with a potential symbiont, and this excitment abates only when the bird sees or hears flying, buzzing bees. Inasmuch as this latter is most apt to happen near a bees' nest, the result is that by following the excited bird the symbiont is usually eventually brought to the vicinity of a bees' nest. The whole behavior works out as if it were purposive, but there is no reason to read any "purpose" or "plan" into it.

It is unfortunate that no intermediate stages in the development of the guiding habit are known. The behavior in *Indicator variegatus* apparently is essentially similar to what we know in *I. indicator*, but is less frequently indulged in, at least with human associates. As our account of the former species will show (p. 111), there is evidence of a very meager sort that the ratel is an associate of the variegated honey-guide as well as of the greater honey-guide.

Cerophagy

The cerophagous, or wax-eating, habit of the honey-guides underlies their interest in bees' nests, and hence is at the base of their "guiding" behavior. Although for many years naturalists had noticed the presence of beeswax in the gizzards of specimens collected, it was not until very recently that it became apparent that it was the wax of the comb and not the bee larvae or the honey or other food stored therein that was the prime desideratum of the birds.

Lest it be questioned at this point that the beeswax as such is the real desideratum rather than the pollen, honey, and larvae in the comb, it should be stressed that we have definite observations showing that when given the choice between dry, empty comb and comb full of honey and larvae the birds seem to prefer the dry wax. In this connection we may recall Culbert's (1947) observations of honey-guides flying into a shed where he kept empty hives fitted with foundation wax and eating this obviously dry, supposedly nonnutritious wax. Mr. Culbert has written me some additional details. He usually prepared all his honey supers and stacked them in sheds at the different apiaries ready for the honey flows. He would leave them open "and the honey-guides would eat the wax as far as they could reach. They also go in the hive entrances if left fully open [that is, hives without bees] and eat the foundation wax up through the frame. I have seen them do it many times." The foundation wax used was made of pure beeswax, not of synthetic substances. Culbert also put a piece of new white comb and a piece of old comb containing bee larvae on a branch of a tree and found the honey-guides ate the new comb but never touched the old one.

Additional instances of these birds feeding on plain wax are not wanting. In Uganda, Pitman (in litt.) recorded two clear-cut cases of honey-guides getting wax by their own efforts. In one case the bird found on a verandah a tin into which wax had been poured. In the other, the bird came into a shed where a swarm of bees had begun to build and then deserted. Recently Cheesman (1952) wrote as follows:

> Two years ago, while putting in new foundation wax, I returned after a temporary absence to find it in shreds. Questioning my native assistant, the blame was put on the honeybirds which were seen perched in the trees nearby. Subsequently I placed an inner cover over the wax super and on my return I was most surprised to find that three honeybirds had gained entrance via the uncovered bee escape well. I was astonished that the honeybird could relish wax which had not a vestige of honey, could detect its presence and find ingress via such a small and awkward hole.

As a still further instance, we may recall that the pioneer of all honey-guide students, the Portuguese missionary Jõao dos Santos, writing in 1569, found this species coming into his little mission church at Sofala to nibble on the beeswax in the candlesticks on the altar. By the time the wax had been melted and formed into candles there could hardly have been any dried pollen or honey or bee larvae left in it. Dos Santos, while recounting what his natives told him of its guiding habits, yet calls the bird "sazu, the bird that eats wax," a clearer and truer statement than any made in the next 375 years.

Native stories, such as one related by Junod (1913, pp. 319–320), suggest that some of the natives may have had some understanding of the birds being interested in the wax and not the honey. Thus, in his account of a Thonga description of the guiding habit, Junod writes: "The fortunate wayfarer can eat to his heart's content and gives the bird the wax. If he wants to be shown a second tree, he has only to burn the wax: the nhalala [honey-guide] not having had its full share of the treat will lead him to another."

These cases raise the question as to how the bird becomes aware of the presence of wax in places where apparently there are no bees flying in and out. To this there is no satisfactory answer as yet. The possibility of their finding it by smell is very slight as birds generally have but poor olfactory acuity. It is conceivable that the birds may have seen humans entering and leaving these structures and followed them to try to lead them to bees' nests; instead, they found stores of readily available wax. In the cases of the barns containing foundation wax, the farmers were bee-keepers and had bees nearby.

In the Umtaleni Valley, eastern Cape Province, observations by C. J. Skead and myself showed a similar but less pronounced preference for wax as compared to honey or bee larvae. We placed a piece of comb containing young bees on a branch and watched a male adult greater honey-guide eating it. The bird went first for the wax and it was not until after nine pieces of wax had been eaten that the first larva was extracted and swallowed. On one occasion, just after a piece of comb had been placed in his favorite call-tree, the bird nibbled bits off the edge of the comb, pausing for fairly long spells to look about him as though he heard something unusual. Then he would take another nibble or might give a series of call notes. The bird ate leisurely and gave the impression of not being hungry, but sometimes he pecked more lustily at the wax, tearing it off and making fragments fly about while he ate small pieces at a time. On another occasion, in the space of three minutes, the same bird (at least a similar adult male at the same perch in the same tree) swallowed nine or ten bits of wax, including a very sizable piece about half or more as large as its beak, and five bee grubs. After it finished eating, it wiped its bill lengthwise on a branch and then flew off and perched on another twig of the same tree and began calling its repetitive *vic-tor* notes.

Credit for suspecting that wax may be a food source to the honey-guides should be given to Moreau (in Sclater and Moreau, 1932, p. 667), who noted that the birds of this family are largely dependent on "wax-producing insects, and swallow quantities of wax with their food; yet the insects providing the staple food of the different genera of the Indicatoridae belong to different orders, and are of an utterly different way of life. It leads one to suspect that wax itself may be utilized by the birds, although it is a material generally regarded as indigestible by animals."

In order to determine whether the honey-guide can and does digest any of the wax it eats, samples of dried comb were saved; later, a bird (*I. indicator*) was shot and its entire digestive tract quickly dried and forwarded to me through the cooperation of D. C. H. Plowes. Subsequent chemical analysis of a piece of the comb, of wax from the gizzard, from the upper part of the small intestine, and from the lower part of the large intestine were made by Dr. A. H. Warth. The melting points and the softening points of the wax were determined with a Fisher-Johns apparatus, an electrical microapparatus consisting of a cylindrical aluminum block in the bottom of which is a spiral hole. This spiral hole contains the heating element, which is shielded by aluminium oxide. "The bulb of a thermometer lies horizontally in a hole bored near the surface of the block. The whole block is surrounded by a bronze ring . . . The substance being tested is placed . . . between cover glasses on an aluminum stage which is likewise electrically heated. A magnifier above the sample makes it possible to see the actual point at which melting takes place. The side armored thermometer is graduated from 20 to 300°." (Warth, 1947, p. 334.)

The results of these tests are tabulated below.

	Temperature in degrees					
	Softening		*Running*		*Fully melted*	
Source of wax	*C.*	*F.*	*C.*	*F.*	*C.*	*F.*
Dried comb	52	126	64	147	67.5	154
Gizzard	54	129	65	149	68	154
Upper part of small intestine	130	266	160	320	170	338
Lower part of large intestine	110	230	119	246	150	302

It will be seen that the wax from the gizzard corresponds closely to that from the dried wild bee comb and is, therefore, interpretable as unchanged. A very abrupt change is to be noted, however, between it and wax from the intestines, which requires more than twice the temperature to begin to soften or to run or to be fully melted. The wax from the upper part of the small intestine has some foreign matter with it, not identifiable with anything from a waxcomb but probably from some of the other food items eaten by the bird. The wax from the lower part of the large intestine is interpretable as consisting of the components of the original wax ingested that were not digested and assimilated. As far as may be judged by tests from the alimentary tract of a single bird it appears that those elements in the wax that have relatively low softening and melting points are assimilated as the material passes into the small intestine.

A word of explanation may be pertinent regarding the fact that the unassimilated components of the wax have softening and melting points so very much higher than the original wax as ingested. Dr. Warth informs me that in beeswax there are some very high melting point components which, when combined with calcium or other inorganic matter, will give extremely high melting point substances. It seems that something of that sort may have transpired in the intestinal tract of the honey-guide.

Further analyses made for me by Dr. F. P. Veitch, Professor of Physiological Chemistry, University of Maryland, yielded the following pertinent information: Two specimens of washed, dried, wild bee comb from South Africa, such as the birds feed on normally, contained silicon, phosphorus, magnesium, aluminium, calcium, copper, iron, sodium, nickel, and zinc; one of them also contained a trace of boron. Other elements not detected by an arc but which may have been present in addition to oxygen were chlorine, sulphur, nitrogen, fluorine, and iodine. Of the elements present, magnesium, phosphorus, silicon, and calcium were found in the greatest quantity; iron, zinc, sodium, and nickel in lesser amounts.

These two samples of bee comb had low saponification numbers, 49 and 45 mg. KOH/gm., the saponification value given for ordinary commercial beeswax being 80. It may be explained that the saponification value or number is the number of milligrams of potassium hydroxide required for the complete hydrolysis of one gram of the wax or other substance being examined. The saponification value varies inversely with the molecular weight of the fatty acids included in the wax. The lower the molecular weights of these constituents the more readily available they are for assimilation as food by the bird eating the substance, so it follows that if any of the wax components were rendered available to the bird, and were assimilated by it during the digestive process, this should be reflected in increasing saponification values of the wax samples from successively posterior portions of the alimentary canal. This is precisely what has been found. Contrasted with the low values of these two samples of bee comb are the results obtained from study of wax from the gizzard of one variegated honey-guide, *Indicator variegatus*, and from the droppings of two lesser honey-guides, *Indicator minor*. Two samples of wax from the gizzard of the first-named species had saponification numbers of 109.3 and 112.4 mg. KOH/gm., while six samples from the droppings of the latter species (captive birds that had been fed on wax and water for several days) revealed saponification numbers of 156.1, 166.6, 167, 177, 200, and 219 mg. KOH/gm. The highest values were from the droppings after only 48 hours of wax-feeding. The relatively high saponification values of the wax from the gizzard and from the droppings indicate that either the microflora of the alimentary canal or the endogenous avian enzymes are capable of splitting these waxes into fatty acids of considerably lower molecular weight, so that it becomes possible for the birds to extract nourishment from them.

The fact that the droppings after only 48 hours of wax eating had higher values than did those from the birds after 72 or more hours of this diet suggests that the birds became progressively hungrier on this unnaturally restricted intake and were thus caused to assimilate a greater percent of the material and probably of the components with the lower rather than the higher molecular weights. It should also be pointed out that little adsorption of fatty materials takes place in the lower part of the digestive tract, and that the higher saponification values of the droppings may reflect continued activity of the micro-organisms on them even after they were excreted by the birds. If, as seems not impossible, some of the wax components had combined in the intestine with calcium salts they would no longer have been adsorbed at all.

In response to my suggestion, Gordon Ranger trapped two live lesser honey-guides and kept them in a cage on a diet of nothing but dried, cleaned beeswax taken from the cappings from cells that had been built on an artificial foundation (manufactured for apiculturists by A. I. Root, Medina, Ohio, and by whom I am informed that these foundations are made of pure beeswax). While wild bee comb contains impurities, especially scleroproteins, it is largely made of wax, and in this case it was probably even less mixed with such foreign materials than usual. One of the birds lived for 29 days, the other for 32 days.

The latter was quite emaciated at the time of death, but the former showed no obvious signs of hunger. Both birds lost some of their equilibrium and were unable to perch for a few days before death, throwing back their heads and giving an impression of "floppiness" of wings and legs. For 11 of the days Ranger weighed the quantity of dry comb given them and it was found that the consumption amounted to 24.8 grams per bird per day.

The bird that died after 29 days had its gizzard full of crumbled wax; the other bird's gizzard was empty, but it had been feeding on wax up through the previous day. The fact that it had been seen eating wax the day before and yet had none in its gizzard suggests that wax is not necessarily retained for some time in the alimentary tract, as might have been supposed, to help account for its almost invariable presence there in wild killed birds. (It had been thought that possibly the birds did not have to get wax as frequently as they do if they were able to hold it in the gizzard for a slow and prolonged digestive process.)

Skead described the symptoms exhibited by the birds during their last days in a letter to Osman-Hill, Prosector of the Zoological Society of London, who replied that the symptoms sounded strongly suggestive of peripheral neuritis or beri-beri caused by deprivation of vitamin B_1, of which the throwing back of the head is a classic symptom. Other elements of the B complex may also have been lacking, as it is rarely the case that only one of the components is responsible. In a state of nature the birds eat insects as well as wax, so this deficiency does not obtain.

While it is inconclusive to argue from analogy, it still seems worth pointing out that the English sparrow, *Passer domesticus*, a bird about the same size as, but wholly unrelated to, the lesser honey-guide can survive without food for only 67.5 hours at 29° C. With a rise in the air temperature from 29° to 46° C. the survival time decreases at the rate of four hours per degree (Kendeigh, 1945). If beeswax were indigestible or without nutritive elements, as the literature suggests, and therefore not to be considered as "food," it would be astonishing indeed that the lesser honey-guide could survive without food ten or more times as long as the sparrow.

It may not be out of place to include here a piece of negative information. During my studies of wax it occurred to me that this material, then supposed to be indigestible, might serve the function of adsorbing certain ions from the digestive fluids in much the same way that some gums and resins are used in human medicine. The Eli Lilly Research Laboratories made the necessary tests for me on beeswax and found it to have no such properties. Commercial white beeswax was exposed to a solution containing sodium, potassium chloride, and phosphate in approximately the same concentration as occurs in the human gastrointestinal tract. This solution was buffered at pH 6.7. A ratio of 2 grams of beeswax to 100 cc. of this solution was used, and after an exposure of one hour with constant agitation no detectable uptake of either sodium or potassium had occurred.

In a recent survey of our knowledge of the chemical aspects of wax, Warth (1947, p. 49) gives the chemical composition of yellow beeswax (of domestic bees) in percentage as follows:

Alkyl esters of fat and waxy acids	72. 0
Free waxy acids	13–13. 5
Hydrocarbons	12–12. 5
Cholesteryl esters of fatty acids (cholesterol palmitoleate)	0. 8
Lactones (myristo-lactone)	0. 6
Moisture	1–2. 0

These figures, it should be remembered, relate to domestic honeycomb. Warth and Hanzley (in Warth, ibid., p. 55) have shown that the composition of the cellular structure of wild bee brood comb differs from that of the ordinary honeycomb made in beehives by bees for storing their excess honey. Analysis of a cleaned brood comb obtained from a wild bees' nest in a hollow tree at Millvale, Pennsylvania, showed that the yield of wax materials, namely beeswax and propolis, was 39 percent, in contrast to over 95 percent from the beehive honeycomb. "After freeing the living quarters of honey, brood, pollen, and other waste materials including leafy matter, the cleaned cells of the comb structure yielded, after wax and propolic extraction, horny shells of sclero-albumenoid, and no cellulose. The nature of the pure wax separated from both types of combs was substantially the same, but the wax extracted by solvent (chloroform) from the brood-comb shows considerably more vegetable wax constitutents, which have not been wholly converted to the end stage."

There is a difference in composition between the wax of the honeycomb proper and the propolis, the wax used by the bees for sealing the cells. Warth gives a succinct comparison of both the comb wax (extraction wax) and the propolis of domestic honeycomb and a wild bees' comb, in percentage, as follows:

	Wild bee honeycomb	*Domestic honeycomb*
Extraction wax:		
Propolis	10. 0	10. 0
Vegetable wax	25. 0	8. 0
Beeswax	65. 0	82. 0
Propolis:		
Propolis resin	92. 7	91. 5
Propolis balsam	7. 3	8. 5

Direct observations in the field of a number of adult honey-guides feeding shows that they eat both the propolis and the honeycomb proper, and more of the latter than of the former. Certainly the absence of propolis in no observable way decreases the avidity with which they eat comb. The fact that they eat foundation wax and candles is further evidence that it is the wax and not any associated resins that they want. That digestion of the wax, or at least of part of it, does take place can no longer be doubted, but the manner of that digestion is not yet clearly understood. There are two methods by which this digestion might be effected: by wax-breaking intestinal bacteria, or by some as yet undescribed and unusually powerful enzyme. While the problem of how the wax is digested is of less immediate concern, as far as the life history of the birds is concerned, than is the fact that this hitherto supposedly indigestible substance is really utilized as a source of food by them, nevertheless it is one of very real interest and is being studied further.

The possibility of bacterial activity is suggested by data on analogous cases of insects that feed on beeswax, such as the waxworms of the microlepidopterous genus *Galleria*, some species of which consume wax as a regular and even large part of their diet, and some roaches of the genus *Blatta* which do so occasionally. Wigglesworth (1939, p. 280) states that the diet of *Galleria* larvae, which feed on honeycomb, consists to a very large degree of wax, and he suggests that "possibly the breakdown of some of the components is begun by bacteria present in the gut." He further writes that the honeycomb is about 60 percent wax, the excreta of the bees about 28 percent wax, and that "part of the wax is certainly utilized. This fraction is variously estimated as 34–43 percent and 50 percent. It is believed to comprise all the alcohol components of the wax, a part of the fatty acids and esters of high molecular weight, but none of the paraffins." With the assistance of Dr. W. Büttiker, who was residing in Southern Rhodesia, some 26 live cultures were made of organisms from the alimentary tract of a greater honey-guide. These were flown to Washington where they were identified and tested by Dr. Joel Warren and Maj. Ray Cowley of the Department of Bacteriology, Army Medical Service Graduate School, Walter Reed Army Medical Center. The strains included *Aerobacter aerogenes*, *Pseudomonas cutirubrum*, *Bacillus firmus*, *Escherichia intermedium*, *Paracolobactrum* sp., and unidentified strains of Enterobacteriaceae and Bacillaceae. None of them showed any evidence of possessing any effect on beeswax or of requiring wax for propagation. These bacterial strains represent the common flora of the gastrointestinal tract of many mammals and birds, and do not necessarily include all of the organisms present in the honey-guide gut, but were the only ones received in viable or uncontaminated condition in Washington.

Evidence for bacterial action in the digestive process is not wanting in other birds, and this further suggests that some such condition may apply to the honey-guides. Thus, Teichmann (1889, p. 235) reports bacteria in the crop of the domestic pigeon that help to break down carbohydrates and to form lactates. Kern (1897) records

Bacterium coli from a number of species of birds, and considers the organism an obligatory intestinal bacterium in birds that feed primarily on plant materials. In his convenient summary Stresemann (1929, pp. 490–491) writes that Scheunert and Schieblich found *B. coli* absent in the rock dove but a milk-souring bacterium (*Streptococcus acidi lactici*) was present. Stresemann further states that the cellulose of plants is not acted upon by ordinary enzymes but is partly digested by the intestinal bacterial flora, which may be largely confined to the caeca. That these bacteria are essential for the normal growth of young birds is indicated by experiments performed by Schottelius. (Current studies (October 1954) reveal a wax-splitting *Micrococcus* sp. and a possibly cerolytic yeast of the genus *Candida* in the alimentary tract of the lesser honey-guide.)

The study of the enzymes present in the honey-guide is also currently under way but no definite results may be reported as yet. It is hoped to further this approach as opportunities permit.

Wax-eating in other birds

While no other birds are known to eat wax, as such, as persistently and in such amounts as the various species of *Indicator* (*Prodotiscus*, on the other hand, is not a beeswax eater, although it gets a waxy substance from the scale insects on which it feeds), there are some other kinds of birds that do consume appreciable quantities of wax-like materials. Many birds that feed on berries inadvertently swallow the waxy coating of these fruits, but it is not known if they actually digest the waxes present. In his account of the food of the North American black-capped chickadee (*Parus atricapillus*), McAtee (1926, p. 86) writes that 30 percent of the food is vegetable matter and that this is largely composed of the mast of coniferous trees and the wax-covered berries of bayberry and poison ivy. Tree swallows (*Iridoprocne bicolor*) and myrtle warblers (*Dendroica coronata*) also eat large quantities of bayberries, especially during the winter months. (Preliminary studies (October 1954) indicate that the wax of bayberries passes unchanged through the digestive tract of myrtle warblers. Further studies are being planned.)

The honey-guides as a family (Indicatoridae) are most closely related to the barbets (Capitonidae). Barbets are not known to eat wax as a regular, or even infrequent, part of their diet, and I cite the following more as a suggestion than as a bit of evidence. C. J. Skead (in litt.) tells me that he was informed by an old native and his son that the black-collared barbet, *Lybius torquatus*, eats beeswax and larvae when it can get them. They seemed very convinced of the accuracy of their report, which was an unprompted one volunteered by them when questioned about the wax-eating habits of the honey-guides. To see whether barbets would eat wax I placed pieces of dried, empty bee comb in the cages of two Asiatic barbets (*Megalaima asiatica* and *M. zeylonica*) in the National Zoological Park, Washington, D. C. For the next two weeks daily observations of the birds' eating bits of the wax were recorded by Malcolm Davis, head keeper of the bird house. This indicated that barbets apparently would eat wax, but there was the disturbing possibility that this might have been, in part at least, a generalized reaction to a strange object introduced into a cage. In order to see how valid this objection might be, similar pieces of bee comb were placed in the cages of a great variety of other birds including a rufous motmot (*Baryphthengus marti*), red-billed pie (*Urocissa caerulea*), Indian crow (*Corvus insolens*), white-backed piping crow (*Gymnorhina hypoleuca*), naked-throated bell-bird (*Chasmorhynchus nudicollis*), three species of turacos (*Tauraco corythaix*, *T. persa*, and *T. leucotis donaldsoni*), and three kinds of guinea-fowl (*Acryllium vulturinum*, *Guttera eduardi schoutedeni*, and *G. plumifera schubotzi*). None of these were ever seen to eat any of the wax although they did peck at it and throw it out of their feeding trays.

The droppings of the two barbets were collected each day and were crudely tested for possible wax content by heating them on the blade of a spatula for melting, and by burning for waxy odor. Most of them proved inconclusive, possibly because of the small amount of wax ingested compared with the total bulk of the food eaten, but a few of them did produce a waxy odor on burning.

Somewhat similar to waxes are plant resins and gums. It may, therefore, be worth mentioning that the giant bustard (*Choriotis kori*) of Africa regularly feeds on the gum exuded from thorn trees of the genus *Acacia* to the extent that its Afrikaans name, "gom paauw," is derived from this habit.

Other birds consume plant gums in smaller quantities, quite unintentionally, and in these cases we have no reason for assuming any nutritive use is made of these substances. To take but a single example, we note that Lucian M. Turner (quoted by Bent, 1946, p. 380) found in Ungava that it was not uncommon for Acadian chickadees (*Parus hudsonicus*) to have their bills covered with gum from spruce and larch trees. He accounts for it "by supposing that during the summer months, when the gum exudes plentifully and is so soft, many insects adhere to it, and when winter comes the birds search for just such places to obtain the insects." The birds probably swallow some of this gum with the insects. Plant gums are largely hydrocarbons.

Somewhat less like wax, but still of interest as comparable materials, are the cambium and bast of trees. In his study of the food habits of the aberrant American woodpecker, the yellow-bellied sapsucker (*Sphyrapicus varius*), McAtee (1911, p. 17) found that these items formed 16.7 percent of its diet.

Another item of suggestive value, even though only inferential in nature, is expressed by "L. S. V. V." (Ibis, vol. 92, p. 330, 1950) in a review of a paper by Fisher and Hinde on "The Opening of Milk Bottles by Birds." He expresses the thought that this recently developed habit may have "started by tits pecking at the waxed tops because of the fat-content." While wax does not have the "fat-content" he seems to assume, it does have a "fatty" texture, which may be attractive to the birds.

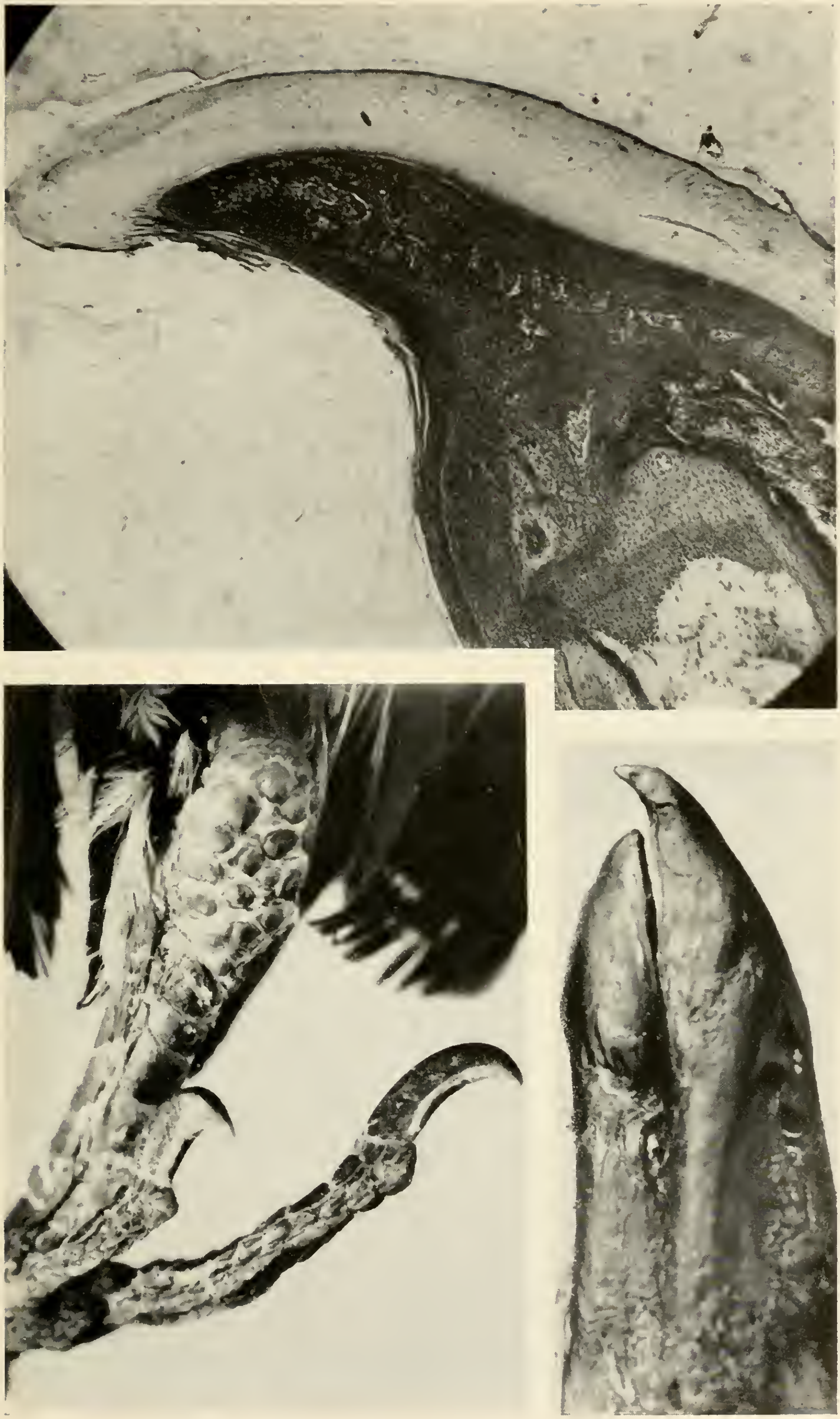
Origin of cerophagy

While it is clear that wax-eating is not wholly peculiar to the honey-guides, it is true that no other birds show such an avidity for beeswax, or consume it for its own sake. How the honey-guides came to feed so extensively on wax is, of course, unknown, but there are some pertinent data worth mentioning here.

Aside from the fact that a peculiar and restricted habit such as cerophagy is hardly likely to have been an ancestral trait, there are two independent bits of suggestive evidence which indicate that probably the group descended from a noncerophagous ancestral stock. One is the fact that honey-guides get no wax in their food until they are practically full grown; the various host species feed the parasitic nestlings on their own diet, which does not include beeswax. Cerophagy therefore seems to be something added to the more ordinary entomophagy common to so many groups of small birds, and not something essential to the growth and development of the honey-guides.

The other line of evidence is the complete absence of any anatomical specializations for wax-eating. Beecher (1953), who dissected a number of honey-guides at my request and compared them with other picarian groups, reports that the heavy jaw musculature of honey-guides is as unspecialized as that of the barbets, but in the honey-guides the bill and its musculature are generally weaker, although the palatine retractors are strong, possibly to give a slightly more powerful bite at the tip of the bill. The honey-guides furthermore show no specialization of the digestive organs, no sign of enlarged palatine salivary glands such as occur in all the nectar-eating groups (Dicaeidae, Nectariniidae, Meliphagidae, and Coerebidae).

In their various phylogenetic branchings the picarian birds show, in a very rough fashion, a correlation between food preferences and family groups; thus, the barbets and toucans are largely frugivorous, the woodpeckers chiefly insectivorous, although there is some overlapping in diet. It seems not improbable that cerophagy, not by itself but in conjunction with a more generalized insectivorous diet, may have helped to set apart, and thus to expedite, the development of that picarian branch that we know as the honey-guides. That this occurred early in their development as a group is indicated by the fact that the existing species nearest to the hypothetical ancestral stock are all wax eaters.



STRUCTURE OF NESTLING GREATER HONEY-GUIDE

Upper: Photomicrograph of section of maxillary hook of 2-day-old bird. Lower: heel (left) of nestling almost ready to leave the nest, showing small naillike scales of rather swollen tarsometatarsus and bill (right) of nestling almost ready to leave nest (photos from Albany Museum, Grahamstown).

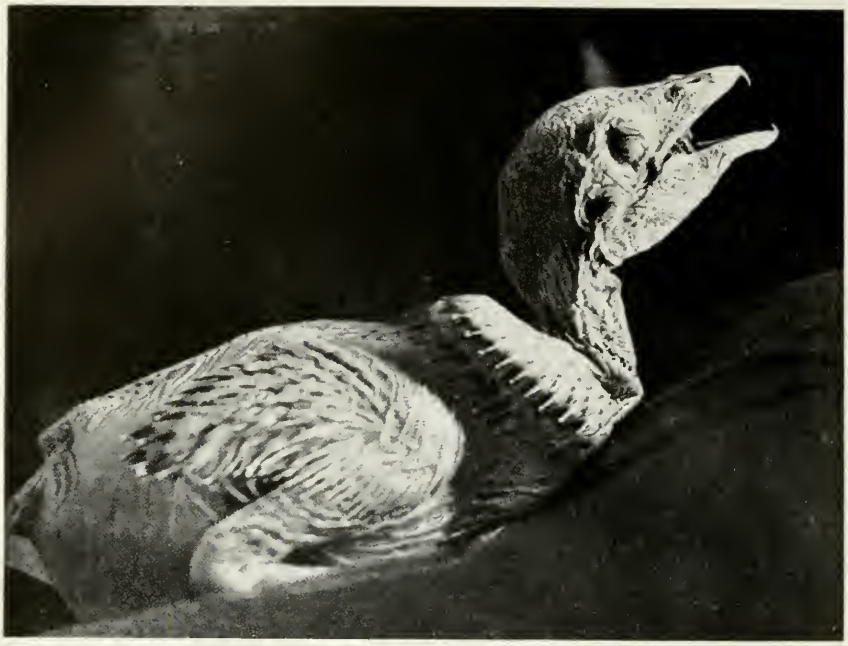
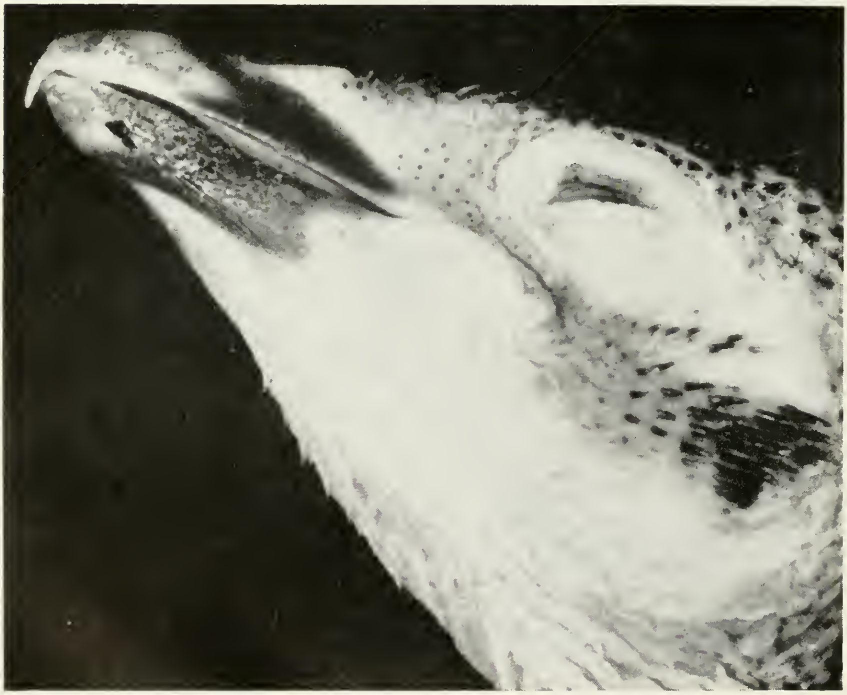
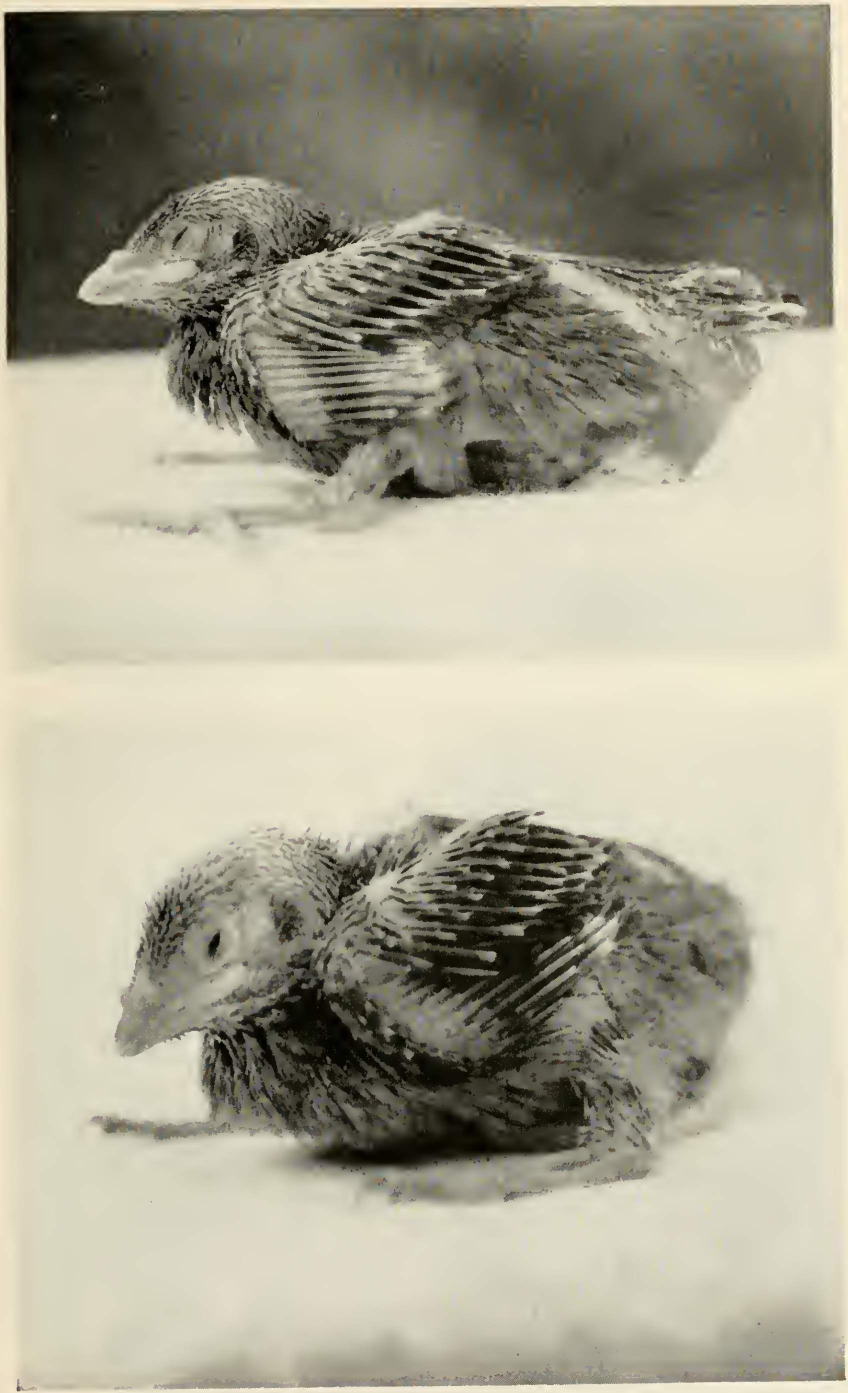


Photo by Haagner and Ivy



BILL HOOKS OF NESTLING GREATER HONEY-GUIDE

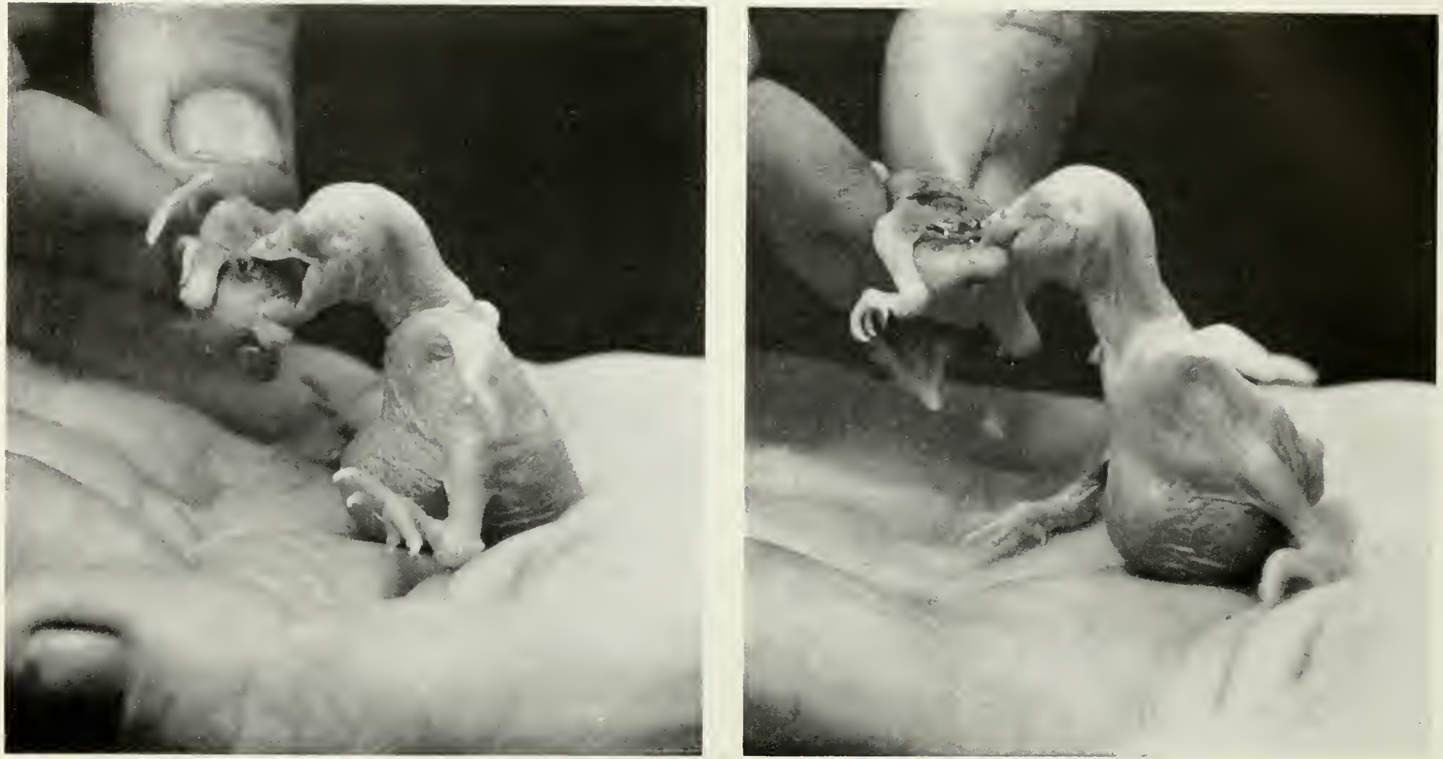
Upper: Bird about 9 days old; lower, bird about 10 to 11 days old (photo of specimen in Transvaal Museum).



Photos by Ranger

LESSER HONEY-GUIDE

Nestling, 16 days old, showing prominent raised rims of nostrils. Hooks have been shed and feathers are partly out of their sheaths.



FOUR-DAY-OLD LESSER HONEY-GUIDE ATTACKING BLACK-COLLARED BARBET NEST-MATE

Left: Grasping barbet with mandibular hooks in attitude typical of that during attacks (note pads of scales on heels of both birds); right: beak closed on barbet (black patches on barbet's back are blood clots from previous attacks).

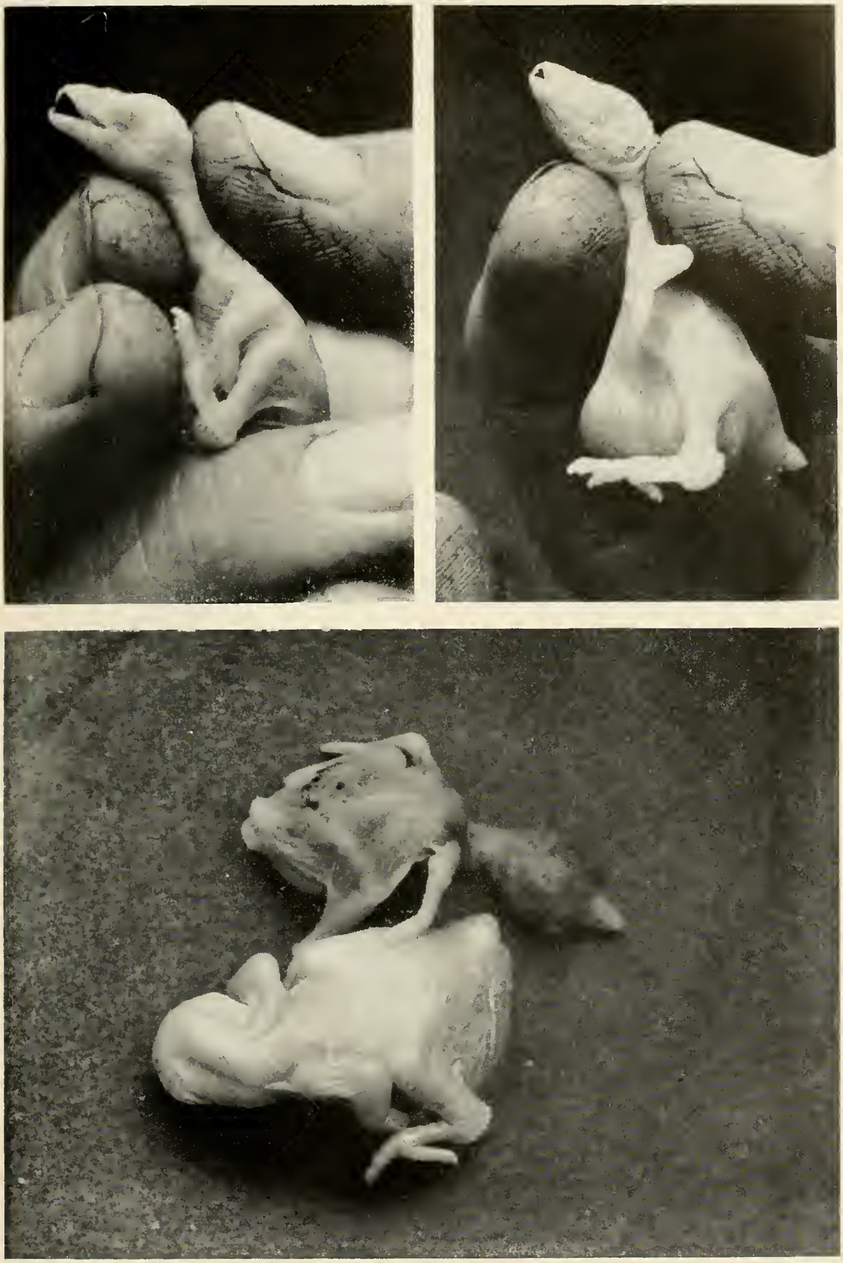
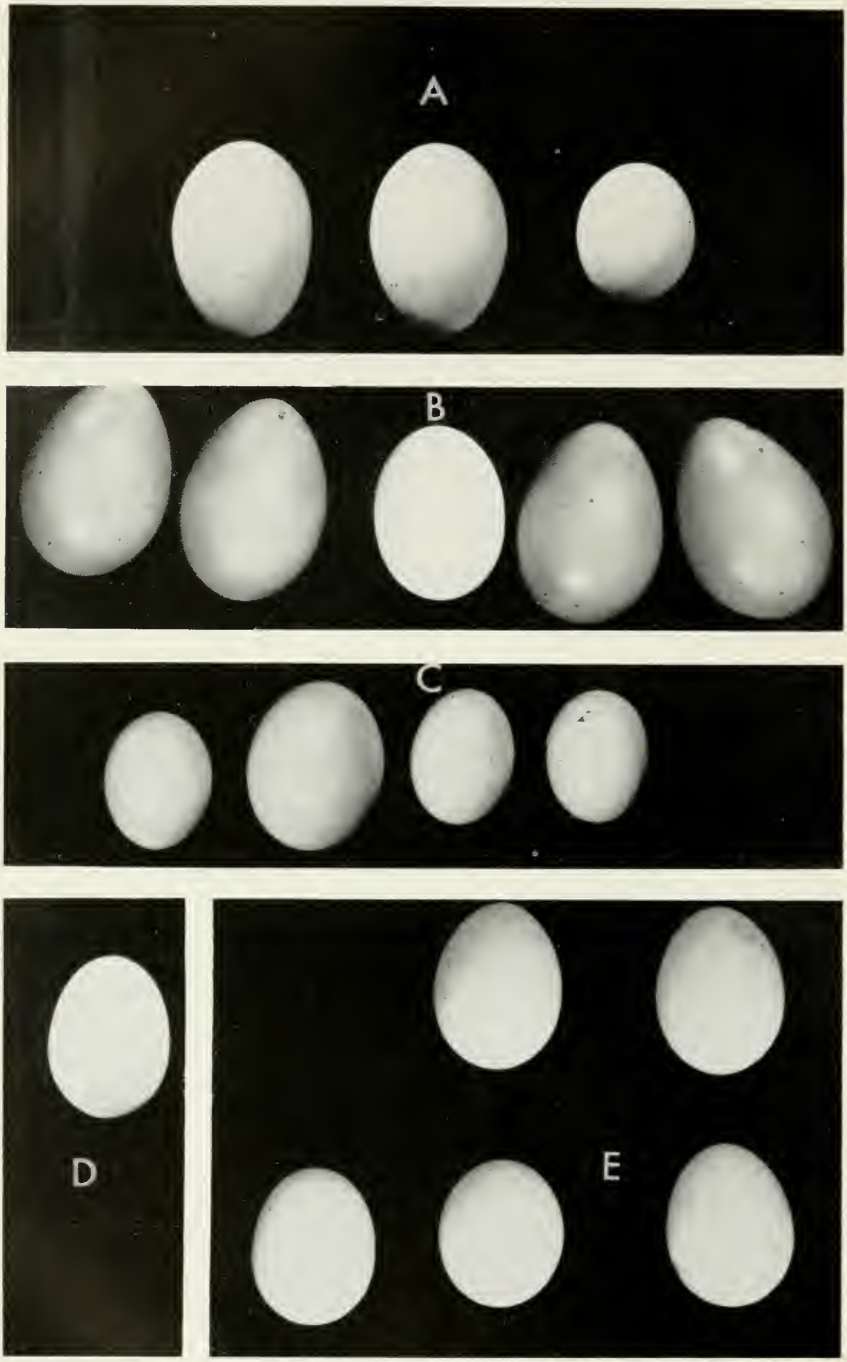


Photo by Ranger

LESSER HONEY-GUIDE

Upper: 3- or 4-day-old nestling, showing bill hooks and heel pads. Lower: 2-day-old nestling with newly hatched black-collared barbet, from same nest, showing skin lacerations on back caused by honey-guide's bill hooks; note relative plumpness of honey-guide and thinness of barbet.



EGGS

Eggs of crested barbet (A) with one of variegated honey-guide; pied starling (B) with one of greater honey-guide; little bee-eater (C) with one of greater honey-guide; lesser honey-guide (D), laid in trap; black-collared barbet (E) with one of lesser honey-guide.

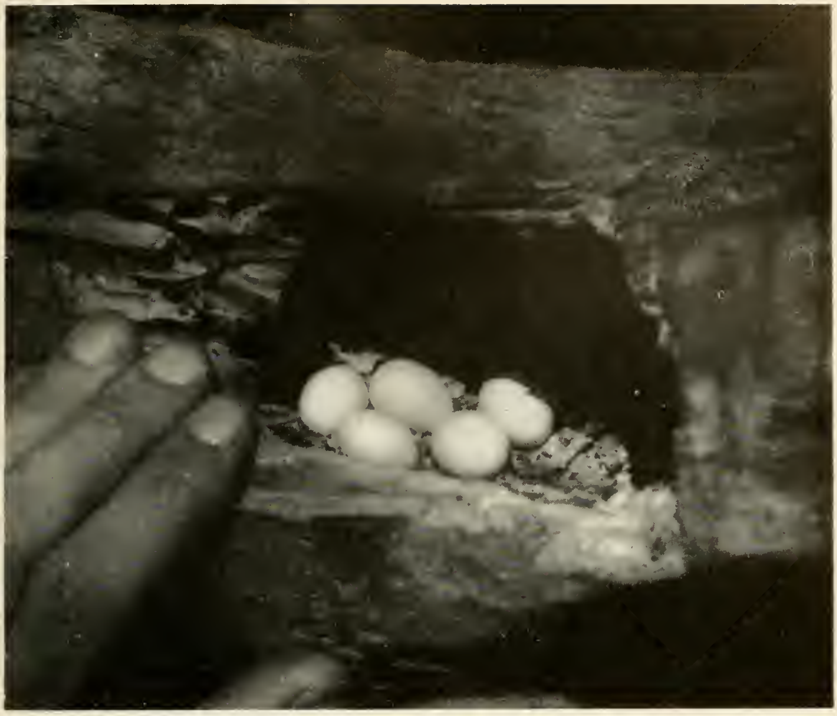


Photo by Plowes

Photo by Ranger

LESSER HONEY-GUIDE

Upper: Opened nest of black-collared barbet containing egg of lesser honey-guide (glossy one, second from left) in addition to four of its own; lower: lesser honey-guide in experimental feeding cage.

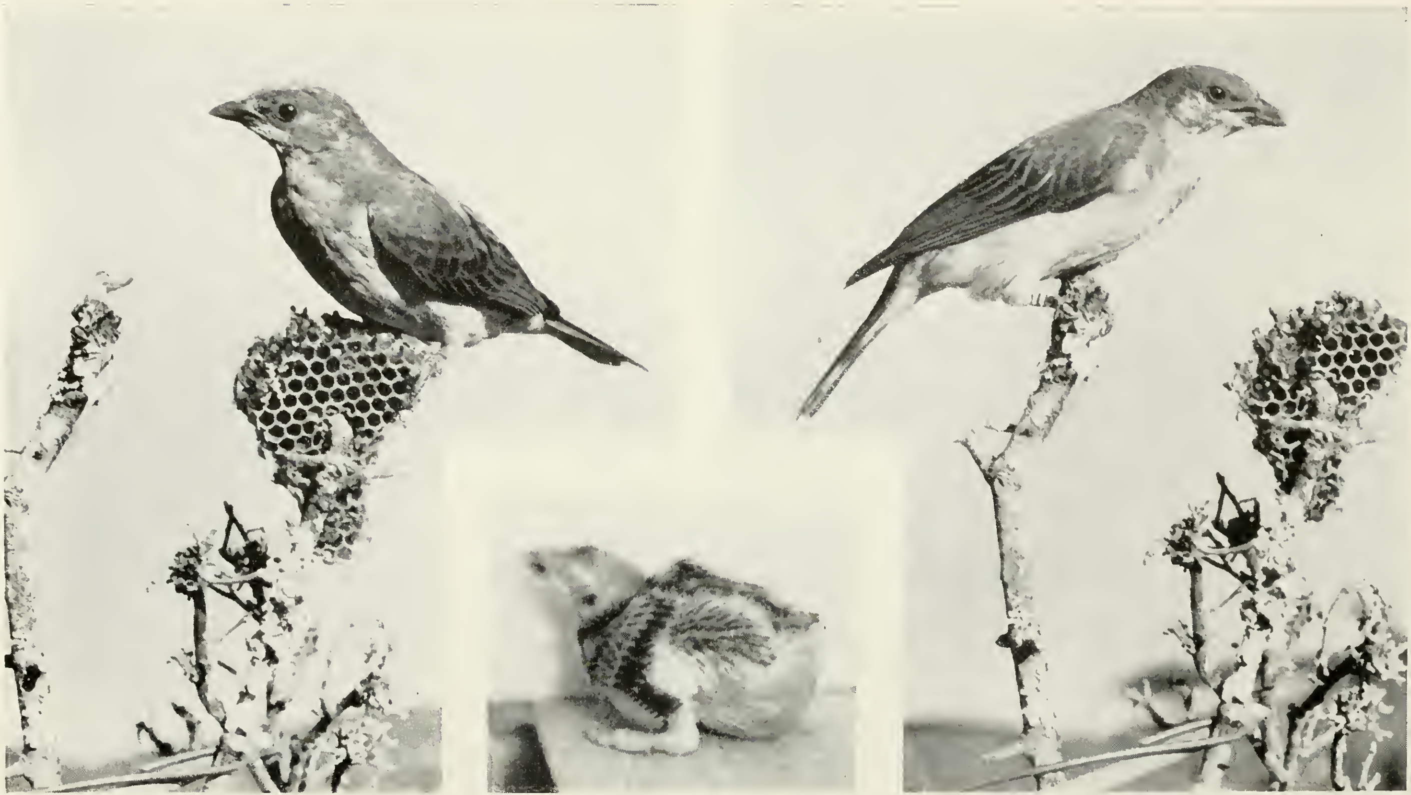
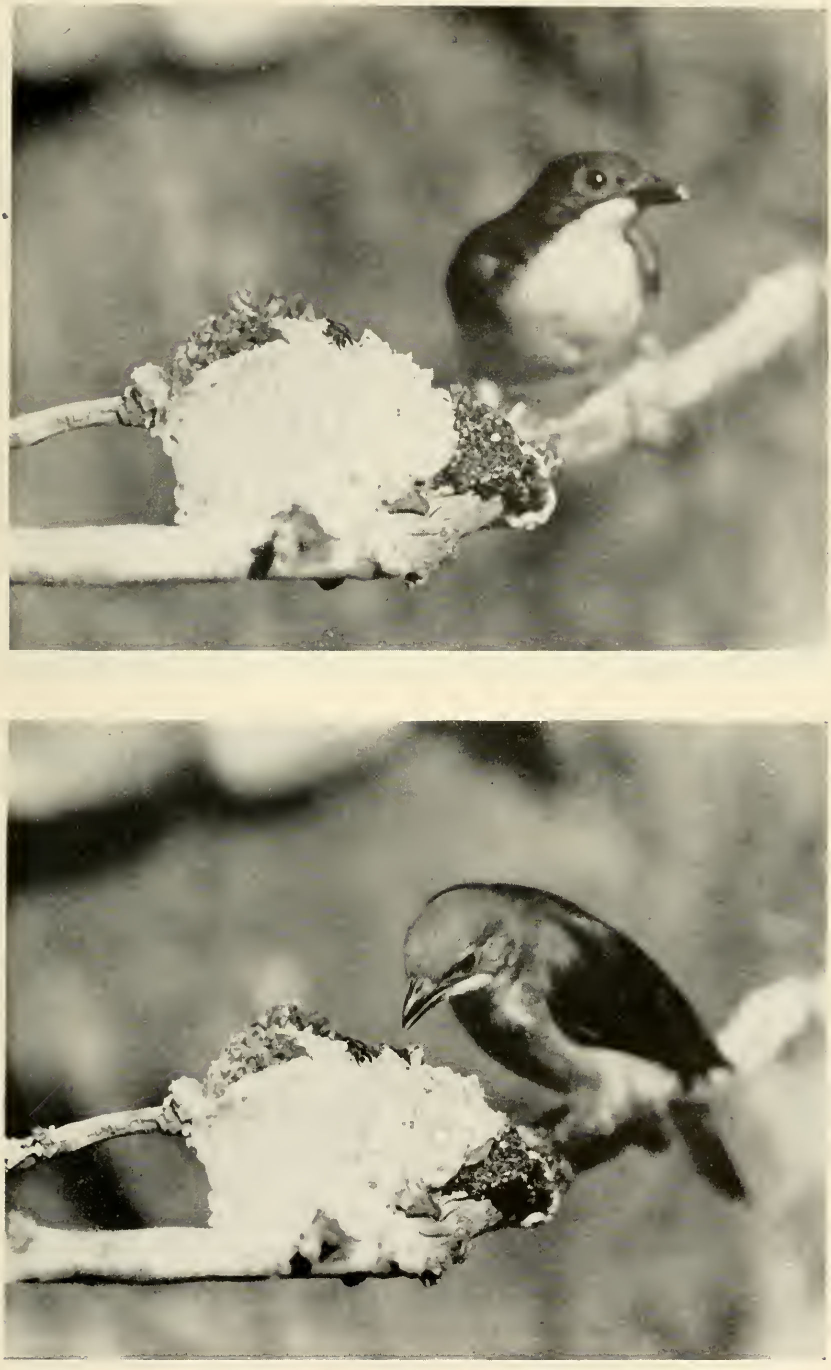


Photo by Ranger Photo by Skead Photo by Ranger

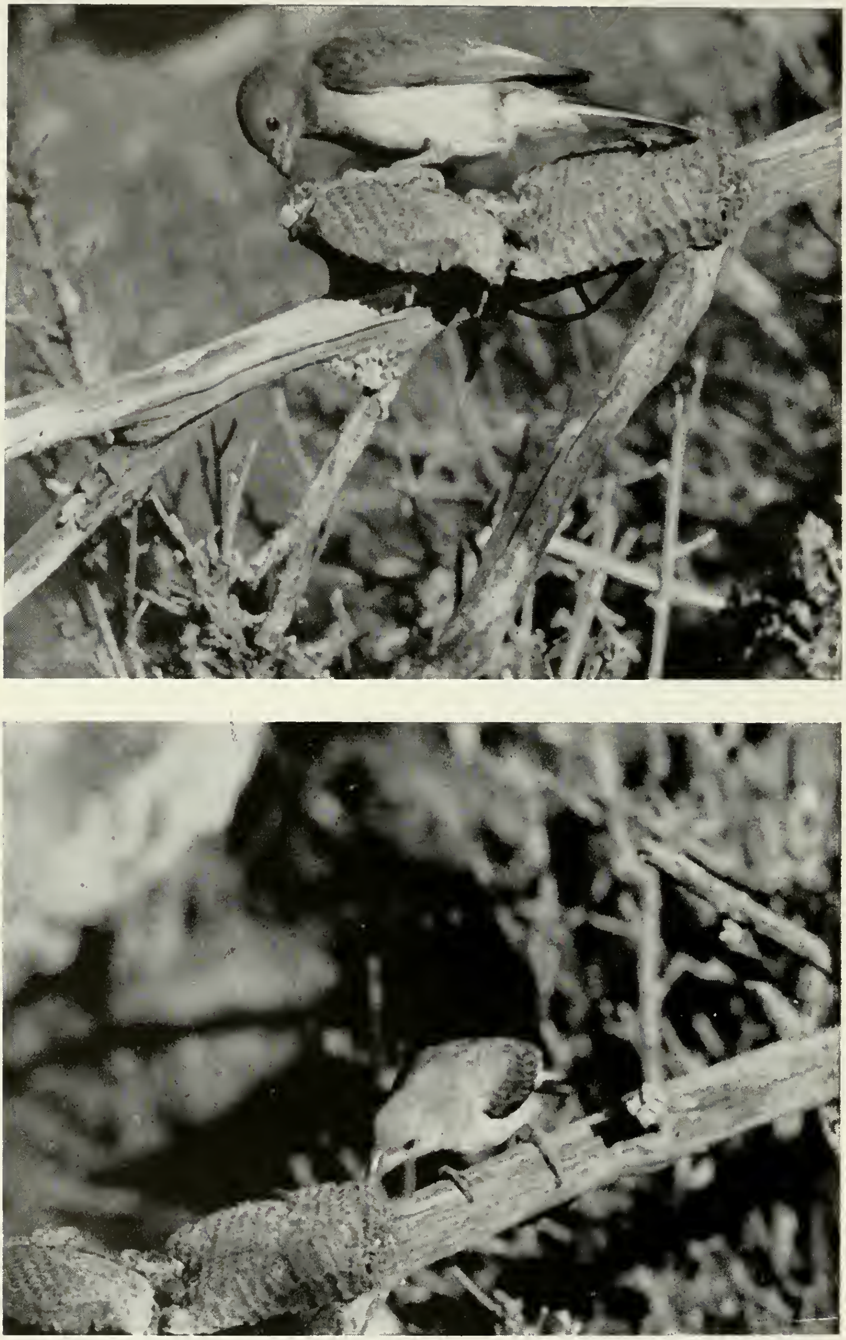
GREATER HONEY-GUIDE

Adult female at bee-comb used as bait; inset: half-grown nestling taken from nest.



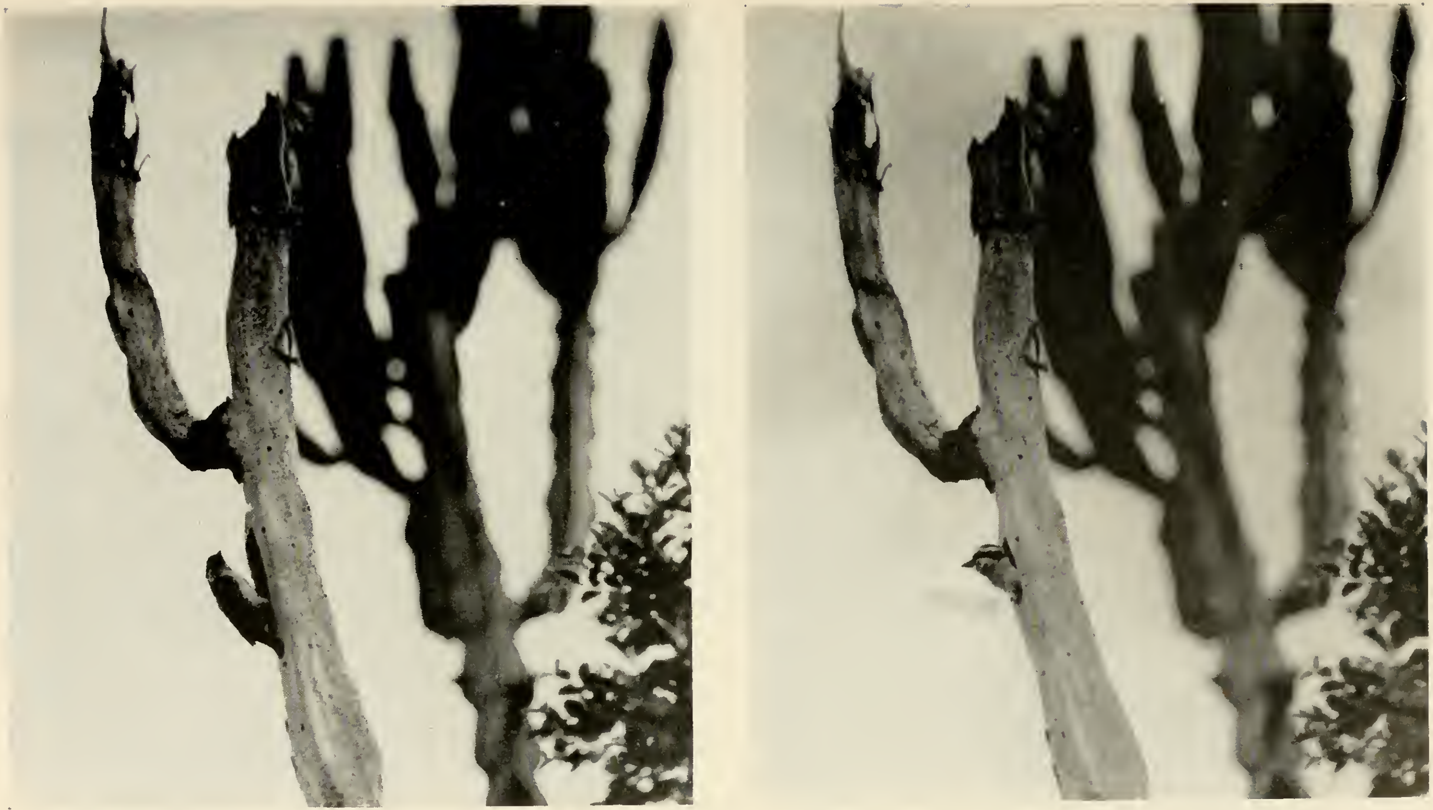
Photos by Ranger

GREATER HONEY-GUIDE FEEDING ON BEE-COMB PLACED IN TREE



Photos by Ranger

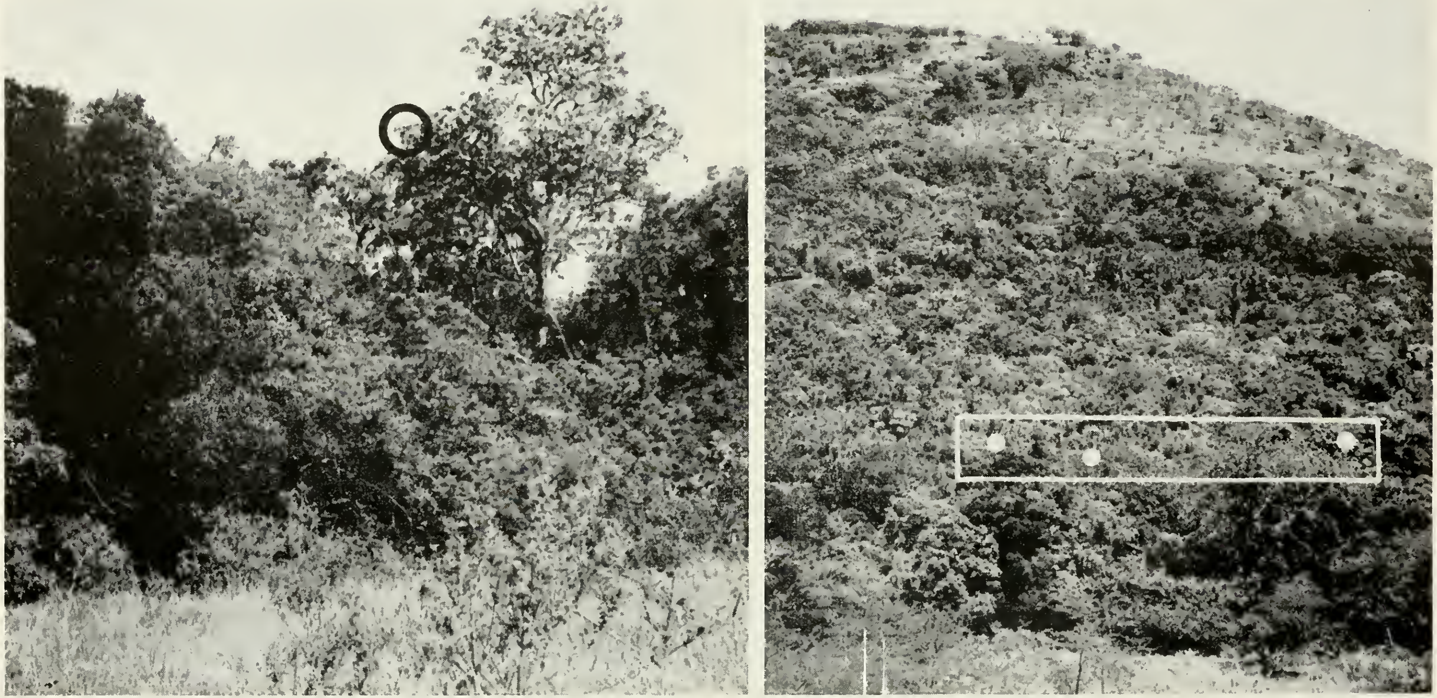
Lesser Honey-Guide Feeding on Bee-Comb



Photos by van Someren

LESSER HONEY-GUIDE

Left: At nesting hole of red-fronted barbet; right: barbet at same hole.

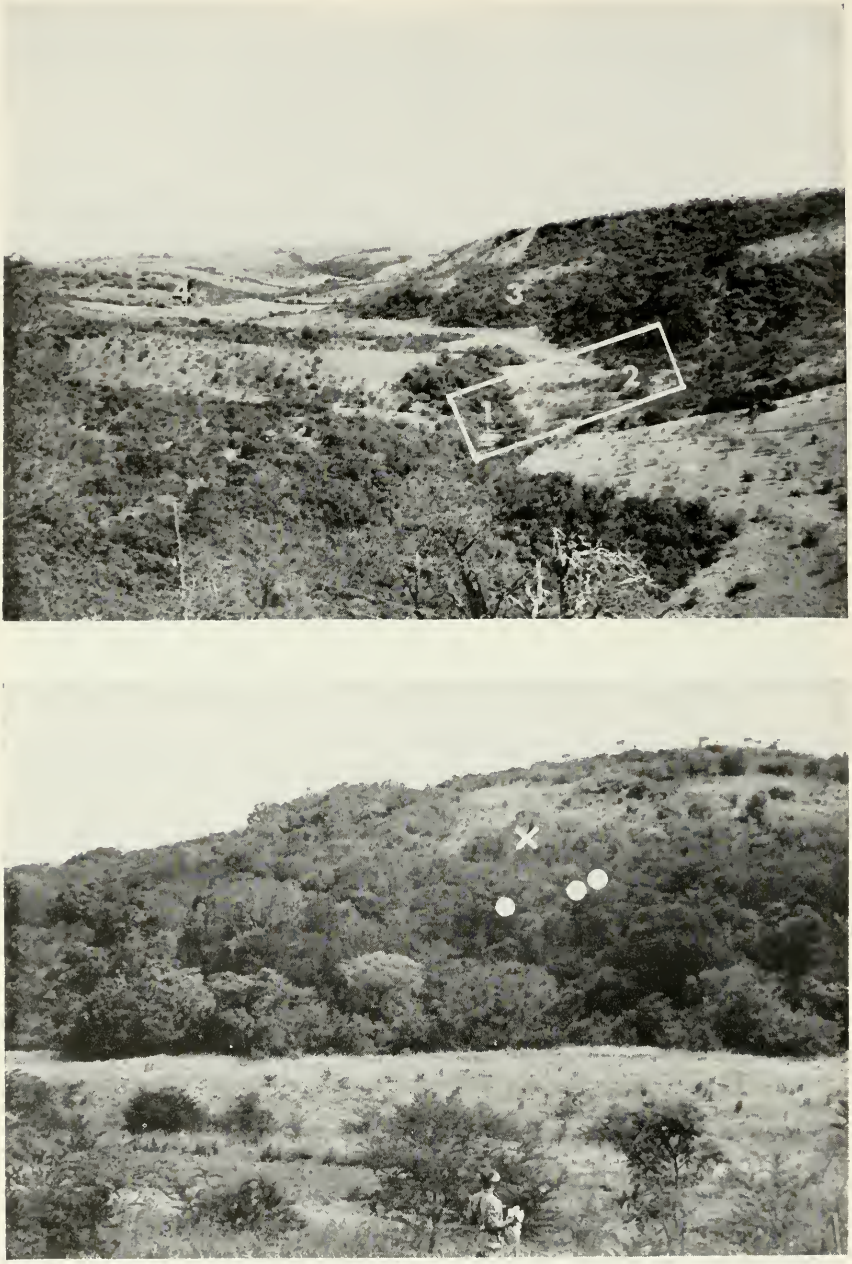


CALL-SITES OF VARIEGATED HONEY-GUIDE, EASTERN CAPE PROVINCE

Left: Favorite call-site (circle); right: the three call-sites used by one bird.

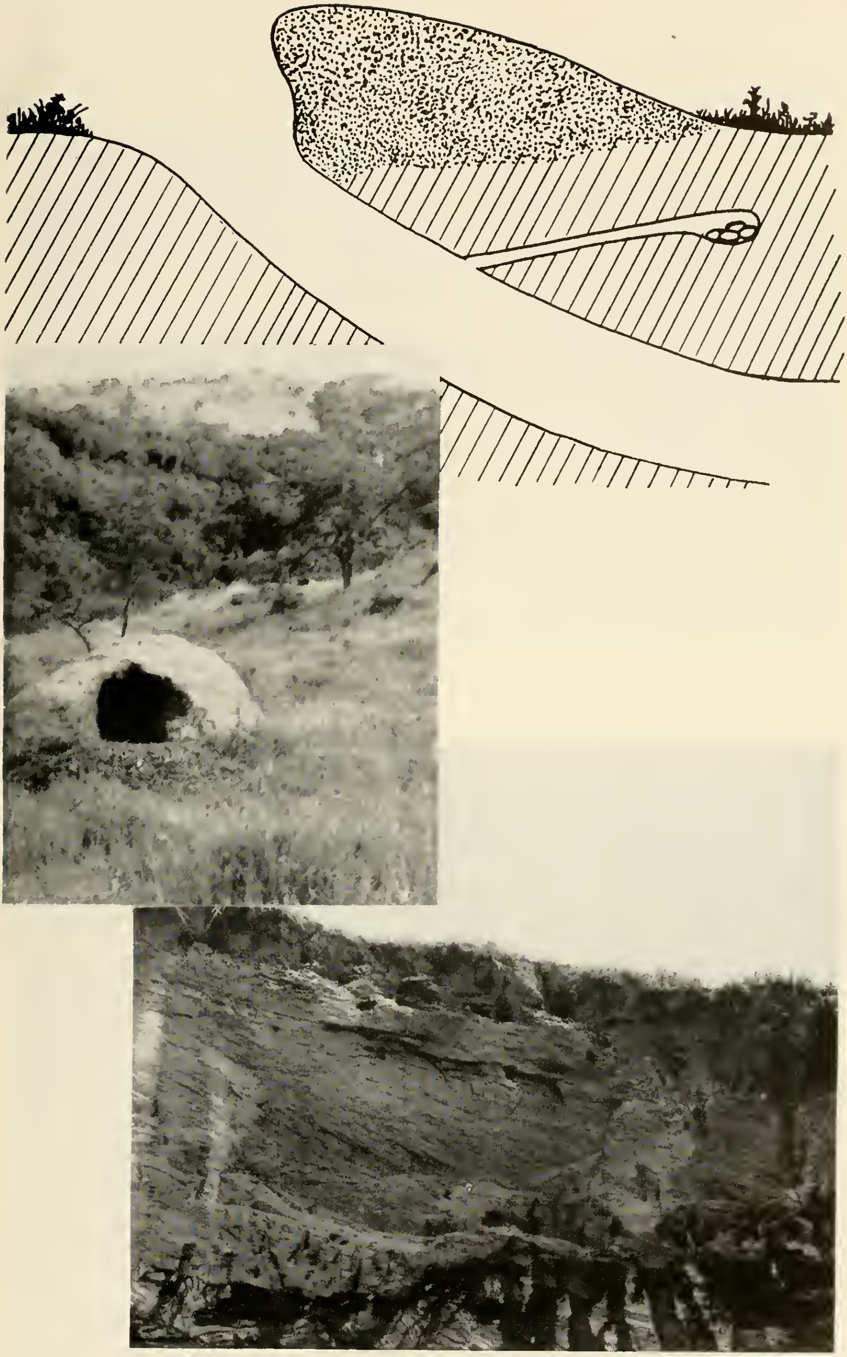
HABITAT OF GREATER HONEY-GUIDE

Upper: Karkloof Gorge, near Howick, Natal. Lower: Regular call-site, Umtaleni, eastern Cape Province.



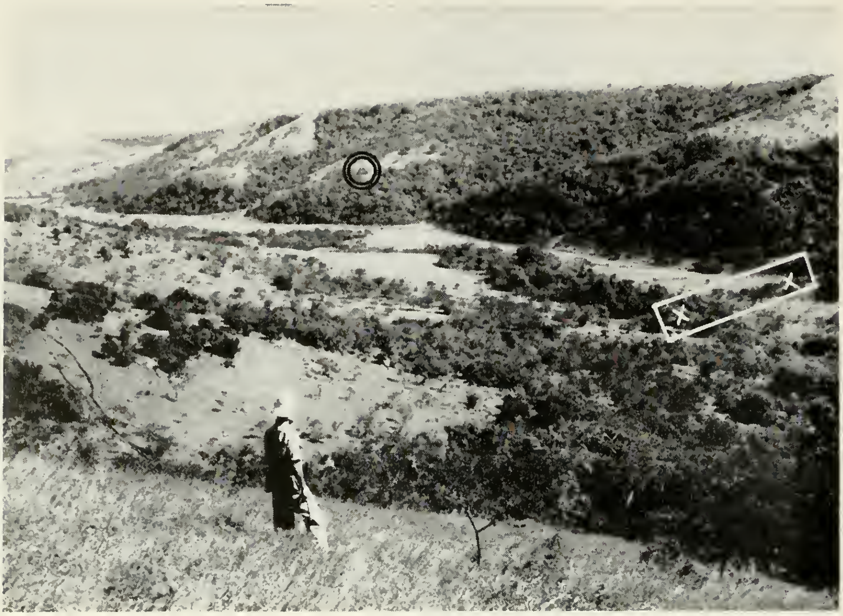
Habitat and Call-Sites of Lesser and Greater Honey-Guides in Umtaleni
Eastern Cape Province

Upper: (1, 2) Favorite and (3) occasional call-sites of a lesser honey-guide; (4) favorite call-site of a greater honey-guide. Lower: Closer view of No. 4, above; "x" marks favorite call-sites of the greater honey-guide, small circles ,the secondary call-sites of the same bird.

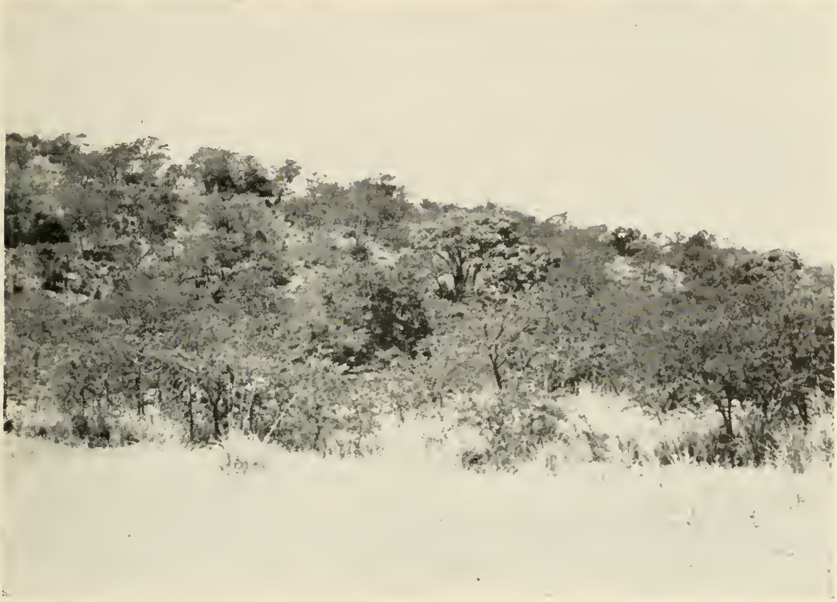


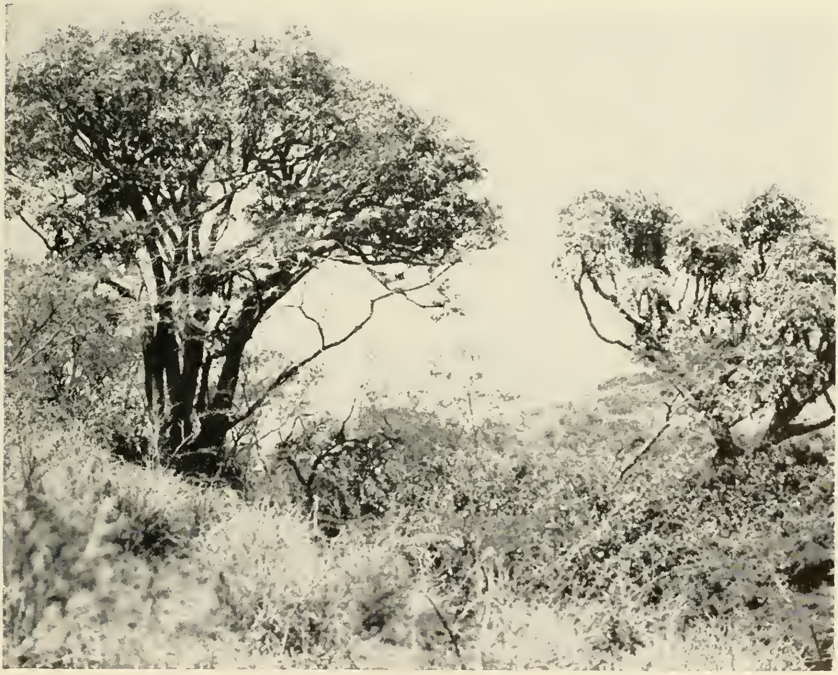
NEST-SITES OF HONEY-GUIDE HOSTS

Upper: Section of aardvark burrow, showing little bee-eater's nest, a frequent repository for eggs of greater honey-guide. Middle: Entrance to aardvark burrow. Lower: Nesting holes, near Howick, Natal, of pied starling, a frequent victim of greater honey-guide.



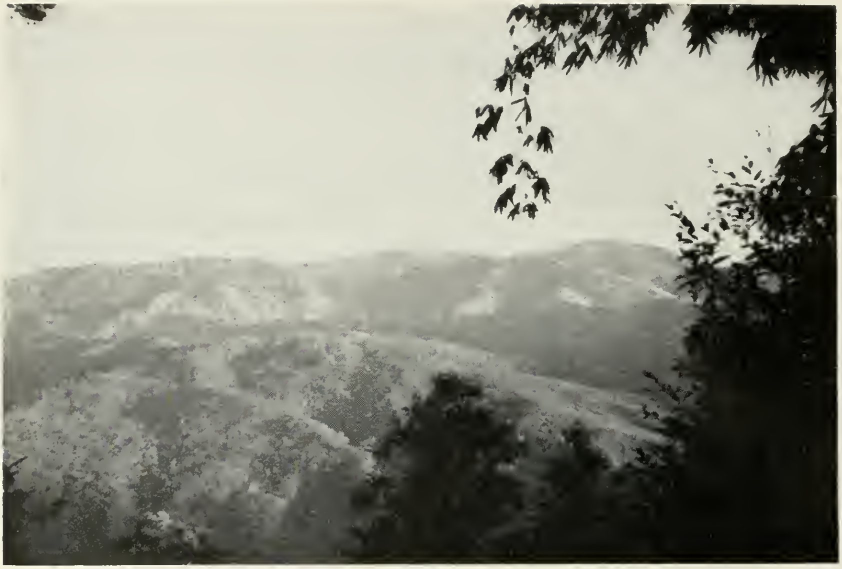
CALL-SITES AND HABITAT OF LESSER HONEY-GUIDE IN EASTERN CAPE PROVINCE
Upper: Umtaleni Valley, showing (right) favorite and (upper center) occasional call-sites; lower: closeup of favorite call-site tree.

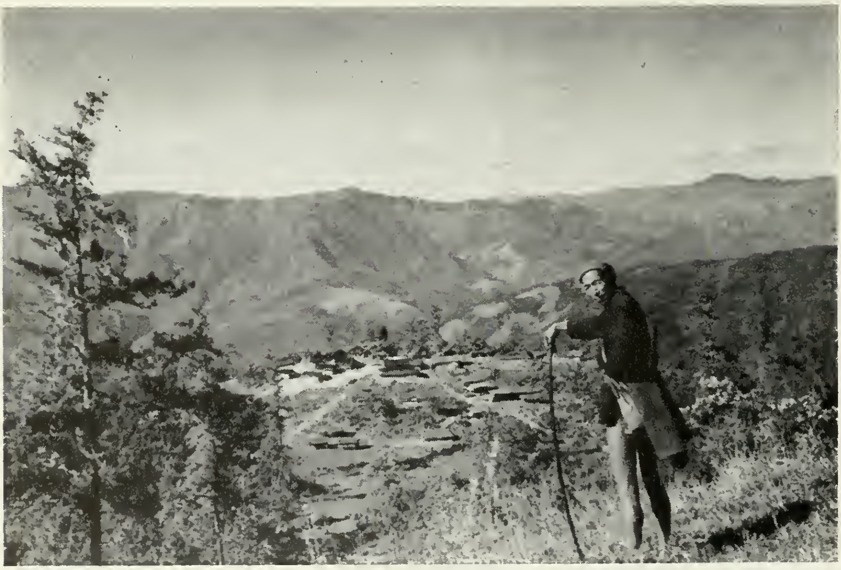




CALL-SITE AND HABITAT OF LESSER HONEY-GUIDE IN EASTERN CAPE PROVINCE

Upper: Primary call-site, tree near center; lower: closeup of primary call-site.





Photos by S. Dillon Ripley

HABITAT OF ORANGE-RUMPED HONEY-GUIDE

Upper: Near Meluri, eastern Naga Hills, near type locality of *Indicator xanthonotus fulvus*. Lower: View from Mount Zephu, eastern Naga Hills, showing typical terrain—patches of mixed deciduous and evergreen forest with cutover scrub, and clearings.

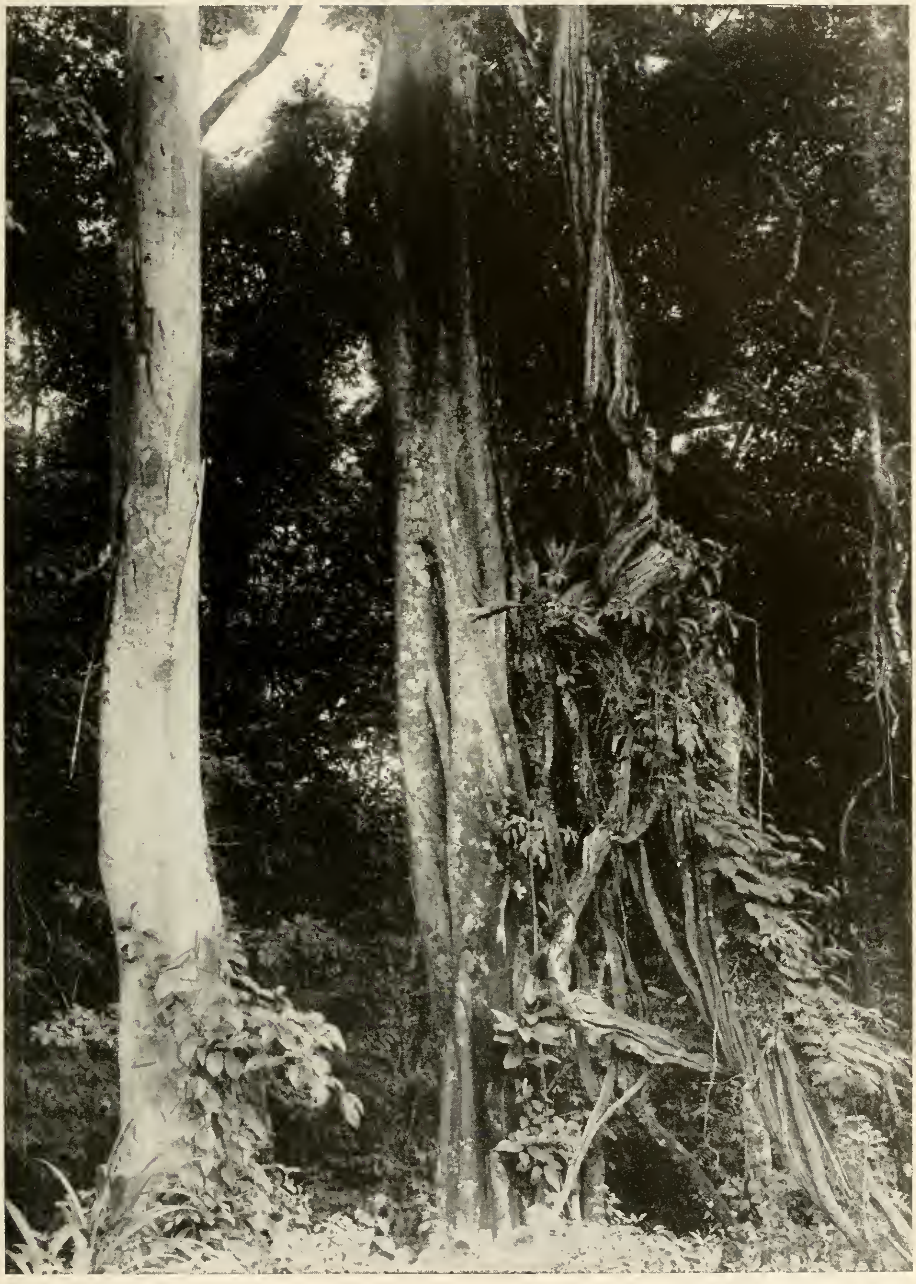


Photo by Herbert Lang

HABITAT OF LYRE-TAILED HONEY-GUIDE—FOREST NEAR POKO, BELGIAN CONGO

Habitat of Sharp-billed Honey-guide in Central Natal

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PLATE 21

Upper left: Slender-billed honey-guide *(Prodotiscus insignis);* upper right: least honey-guide *(Indicator exilis);* center: variegated, or scaly-throated, honey-guide *(I. variegatus);* lower left: Zenker's honey-guide *(Melignomon zenkeri);* lower right: Malayan honey-guide *(I. archipelagicus).*

PLATE 22

Greater honey-guide *(I. indicator)* and ratel *(Mellivora capensis).*

PLATE 23

Upper left: Orange-rumped honey-guide *(I. xanthonotus);* upper right: lyre-tailed honey-guide *(Melichneutes robustus);* left center: greater honey-guide *(I. indicator);* lower left: sharp-billed honey-guide *(Prodotiscus regulus);* lower right: spotted honey-guide *(I. maculatus).*

PLATE 24

Lesser honey-guide *(I. minor)* being driven by black-collared barbets *(Lybius torquatus)* from their nesting hole.

PLATE 25

Female greater honey-guide *(I. indicator)* at nesting hole of a pair of violet-backed starlings *(Cinnyricinclus leucogaster).*

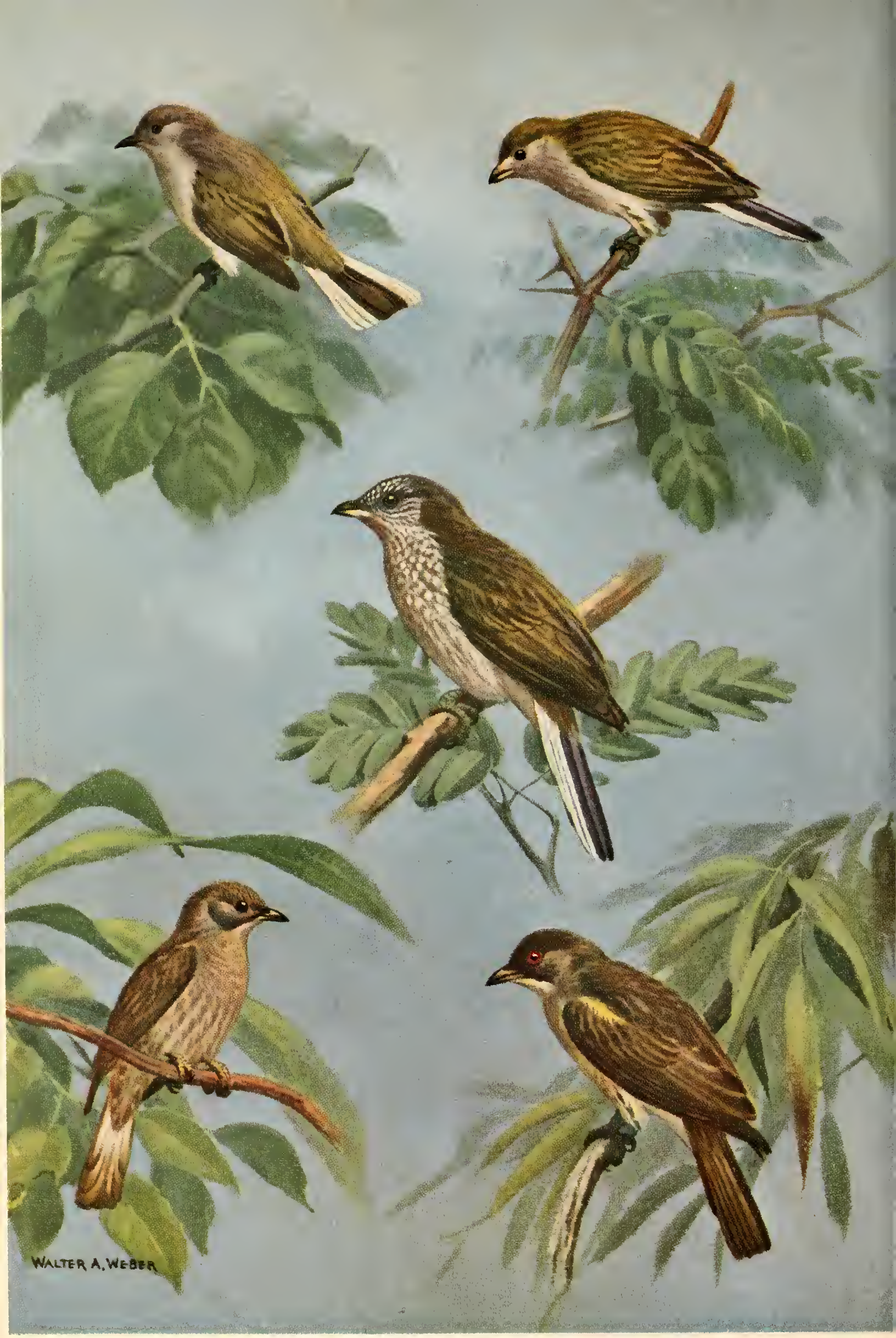
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PLATE 21

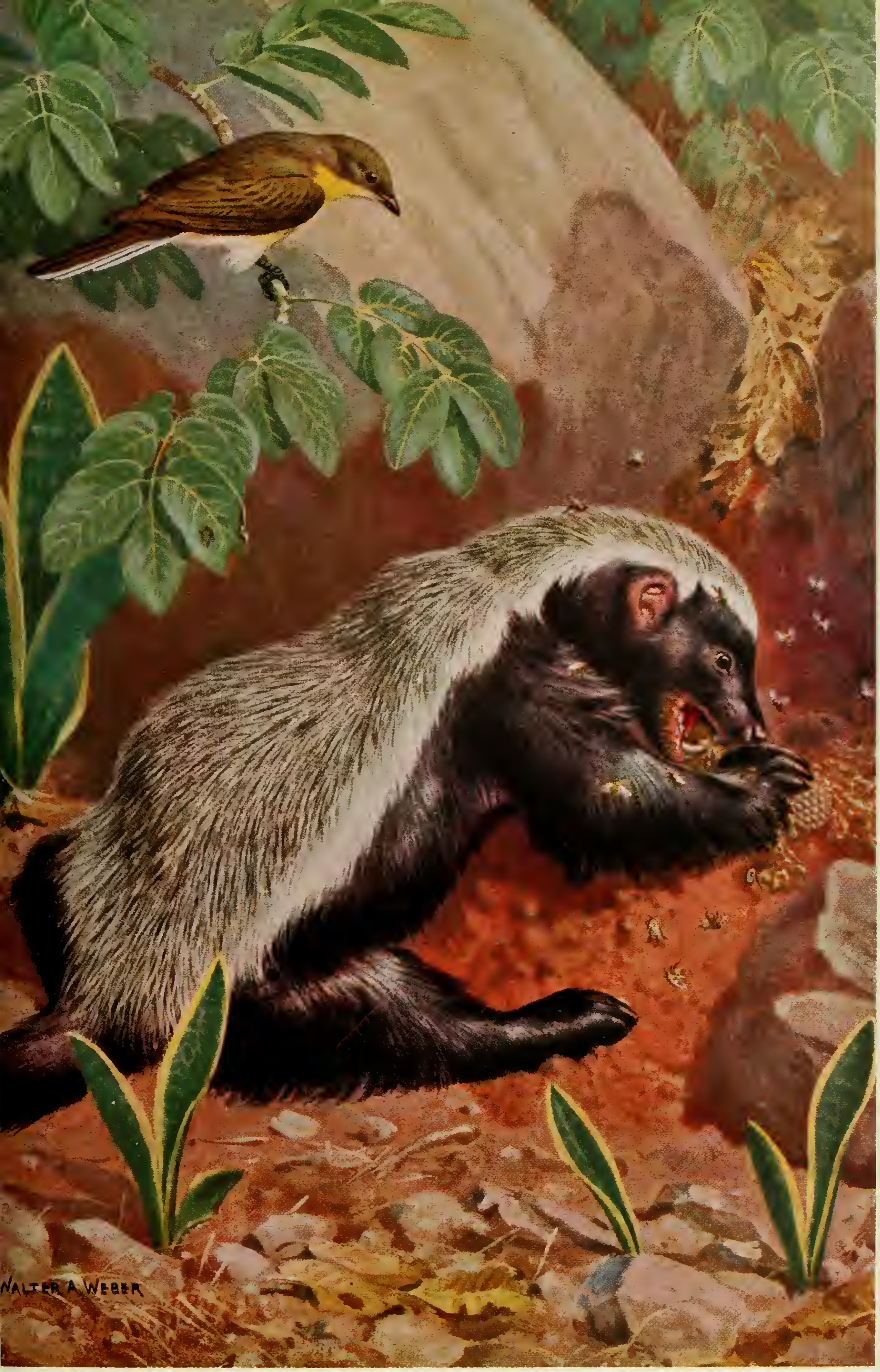
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Plate 22

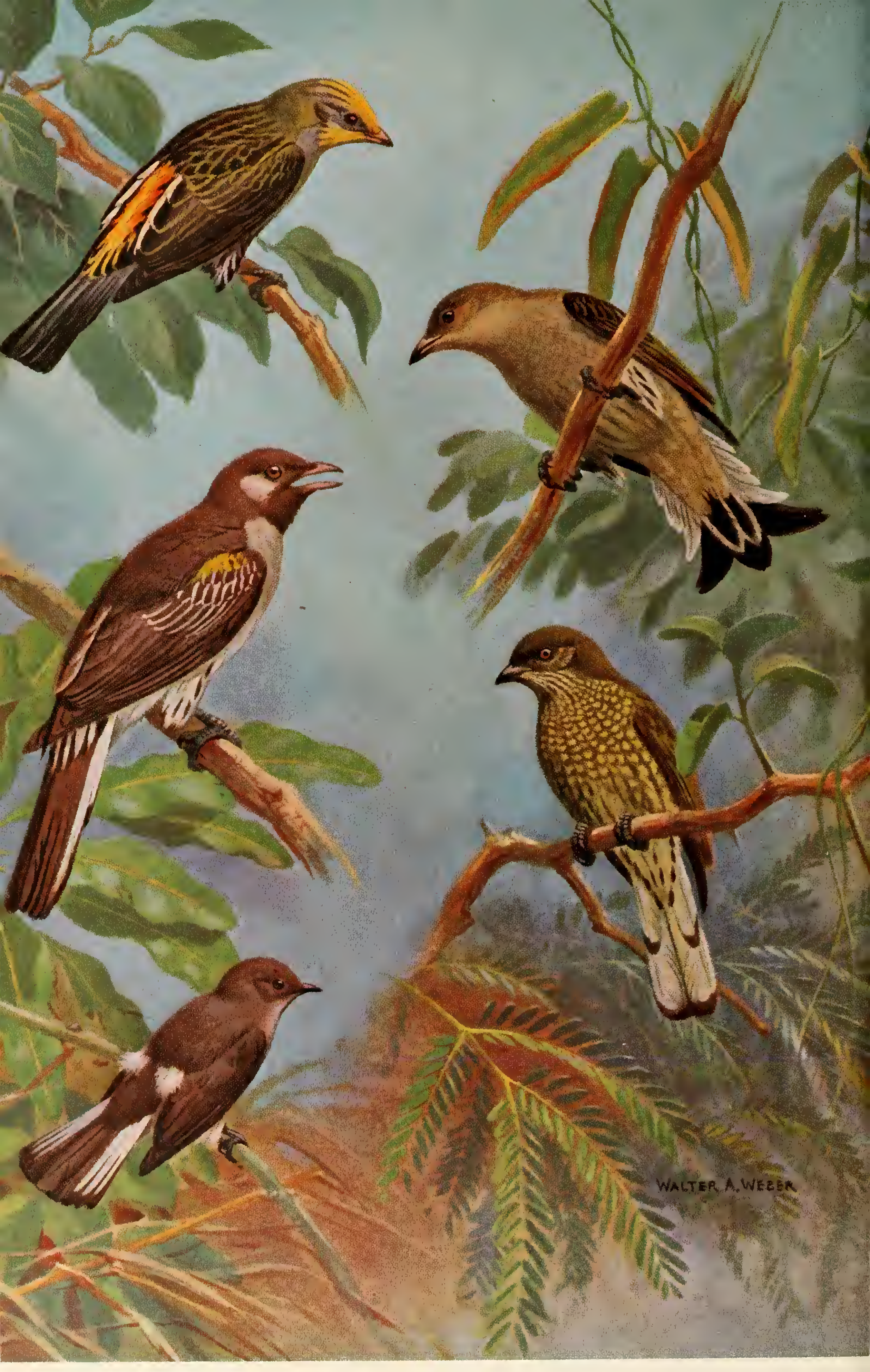
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PLATE 23

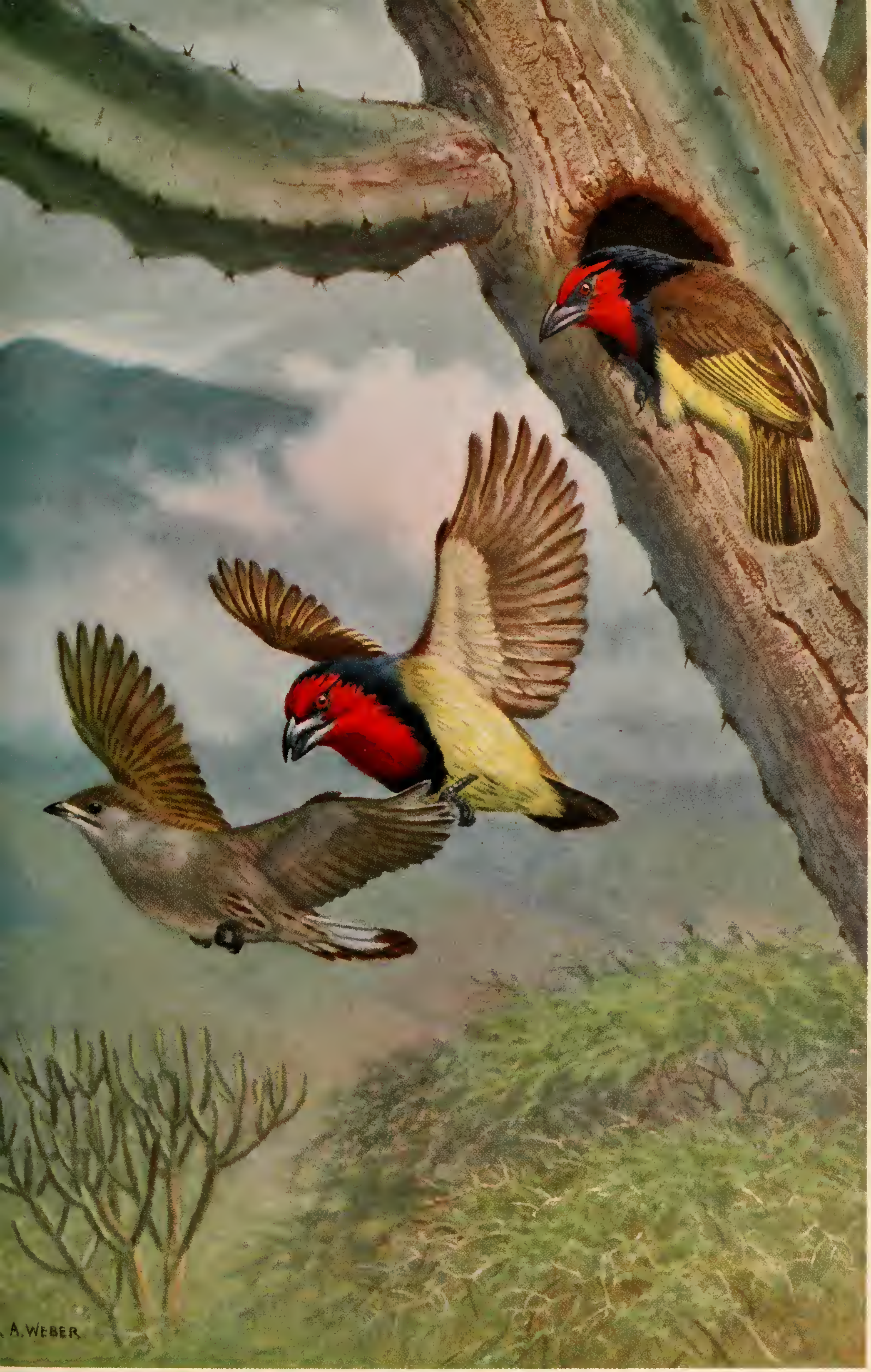

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Plate 24

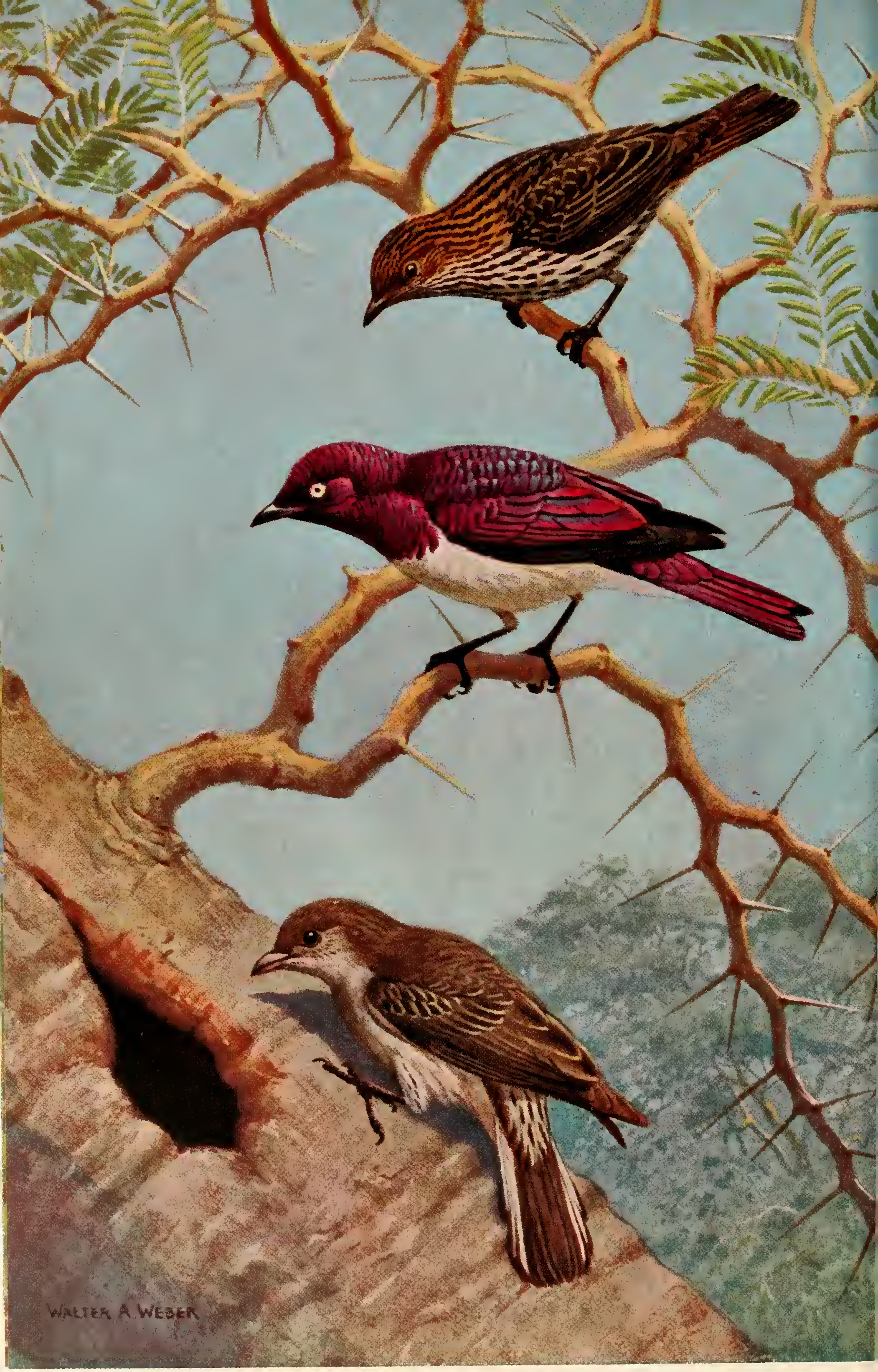
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PLATE 25

The species of honey-guides

Genus *Indicator* Stephens

Indicator STEPHENS, *in* Shaw, General zoology, vol. 9, pt. 1, p. 131, 1815. (Type by tautonymy, *Indicator sparrmanii* Stephens=*Cuculus indicator* Sparrman.)

Prodotes NITZSCH, Observationes de Avium arteria carotide communi, p. 15, 1829. (Substitute name for "*Indicator auctorum.*")

Melignothes CASSIN, Proc. Acad. Nat. Sci. Philadelphia, vol. 8, p. 156, 1856. (Type, *M. conirostris* Cassin.)

Melignostes HEINE, Journ. Ornith., vol. 8, p. 192, 1860. (Emendation for *Melignothes* Cassin.)

Pseudofringilla HUME, Stray Feathers, vol. 1, p. 314, 1873. (Type by original designation, *Indicator xanthonotus* Blyth.)

Pseudospiza SHARPE, *in* Rowley, Ornithological miscellany, vol. 1, p. 207, 1876. (New name for *Pseudofringilla* Hume.)

Melipodagus ROBERTS, Ann. Transvaal Mus., vol. 8, p. 220, 1922. (Type by original designation, *Indicator variegatus* Lesson.)

"Typical" honey-guides, characterized by having a tail of 12 feathers, outer 2 pairs shorter than the others (the outermost the shortest), median 4 pairs equal in length; bill varying from fairly large and strong to short and stubby, but never slender. Three fairly distinct subgenera may be recognized: *Indicator*, with a large and strong bill, four species, three (*I. indicator*, *I. variegatus*, and *I. maculatus*) in Africa and one (*I. archipelagicus*) in Malaya and the East Indies; *Melignothes*, with a short, stout, blunt bill, and smaller general size than subgenus *Indicator*, two species (*I. minor* and *I. exilis*), each with several races, in Africa; and *Pseudofringilla*, a remarkably colored species with a finchlike bill, one species, *I. xanthonotus*, of the Himalayas.[15] The guiding habit is confined, as far as known, to the subgenus *Indicator*.

The breeding habits of four of the seven included species are known, being parasitic chiefly on hole-nesting birds; breeding habits of the other three species probably are similar.

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[15] The genus *Melignomon*, retained in this work as in current literature for one species, *M. zenkeri*, is hardly more than a fourth subgenus of *Indicator*. Because of its intermediate position between *Indicator* and *Prodotiscus*, it is convenient to have a distinct name to use for it in our discussions.

Key to the species of Indicator

a^1. Tail with the basal half or more of the three outer rectrices white.
  b^1. Rump and upper tail-coverts white, with or without dark streaks.
Indicator indicator
  b^2. Rump and upper tail-coverts with no white.
    c^1. Throat and breast with light spots on a grayish or olive ground color, or spotted or streaked with dusky.
      d^1. Crown and back olive in adults, olive brown in young; spots on upper breast rounded, yellowish, on an olive ground; abdomen yellowish.
Indicator maculatus and races
      d^2. Crown grayish to grayish olive, with whitish lines on forehead; back olive, spots on upper breast less distinct, less yellowish, the feathers often appearing more streaked or spotted in the middle with grayish; the abdomen whitish without spots or streaks.
Indicator variegatus and races
    c^2. Throat and breast uniform grayish with no spots of lighter.
      d^1. Size smaller; wing less than 80 mm . . . . . **Indicator exilis** and races
      d^2. Size larger; wing 80 mm, or over . . . . . **Indicator minor** and races
a^2. Tail with no white on the basal half of the outer rectrices.
  b^1. With a large patch of bright orange-yellow on the rump.
Indicator xanthonotus and races
  b^2. With no patch of orange-yellow on the rump . . . **Indicator archipelagicus**

Spotted Honey-Guide

Indicator maculatus G. R. Gray [16]

FIGURES 1, 2,*a*, 3,*e*; PLATE 23

DISTRIBUTION

A poorly known bird of the heavy forests of tropical West Africa, this honey-guide ranges from Gambia and Portuguese Guinea through Sierra Leone, Liberia, Gold Coast, Togoland, Nigeria, Cameroon, Gaboon, and eastward across the upper Belgian Congo to extreme western Uganda. It has not been reported, as yet, from Ivory Coast. The species comprises two morphologically distinguishable races, a western Upper Guinean race, typical *maculatus*, and an eastern, Lower Guinean (Cameroon and Gaboon eastward) race, *stictithorax*. The known localities of occurrence of the two are as follows.

Indicator maculatus maculatus: Gambia (Gambia River), Portuguese Guinea (Farim, Rio Cassine, Gunnal), Sierra Leone (Bafin River, Bagbwe Valley, near Bintimane Peak, Karene Province), Liberia (Sofori Place, Hill Town), Gold Coast (Monse Hills, Kwissa, "between Cape Three Points and Accra," and Dabocram, Ashanti), Togoland (Kratji), and Nigeria (Ondo).

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[16] *Indicator maculatus* G. R. Gray, Genera of birds, vol. 2, p. 451, pl. 113, 1847. (No locality; the type in the British Museum is from Gambia.)

Indicator maculatus stictithorax:[17] Cameroon (Mount Cameroon, Efulen, Bitye, River Ja, Yabassi, Kribi, Old Port Cameroon, Kupé Mountain), Spanish Guinea (Alén, Afán Otóng Nguíng near N'Koumadjap), and Gaboon (Oyem, Kango, Ogowe River), across the forested area of the Belgian Congo (Loemma River on Loanga Coast, Gudema, Ira River, Beni, Ukaika, Simbo, Kamituga, Angumu, Lutunguru, Ngumba, Mabóya, Ikela, Iyonda, Gamangui, upper Kibali River) to extreme western Uganda (Bwamba forest). This race differs from the nominate one in being more yellowish on the abdomen; the light pectoral spots are more distinct, and the crown is somewhat paler, the cheeks and malar region streaked with yellowish. The two races are alike in size.

Our knowledge of the life history of the spotted honey-guide is very meager indeed, as may be seen from the following compilation of the available data. I have had no personal experience with this bird in life.

Breeding Season

Indications of breeding season are given by the following recorded data.

Sierra Leone: Near Bintumane Peak, March 7, male with enlarged testes collected.

Spanish Guinea: N'Koumadjap, early January, egg collected.

Cameroons: Kupe Mountain, November 19, female with enlarged ovary collected.

Uganda: Mongira, Bwamba Forest, March 22, male in full breeding condition collected.

Eggs and Egg Laying

Only a single egg attributed to the spotted honey-guide is known. The circumstances attendant on it are as follows. Early in January 1952 Jorge Sabater trapped a female spotted honey-guide and when he went to inspect the bird he found a fresh, unbroken, pure white egg just below the trap. He had not actually seen the bird lay the egg, but felt that there was no reason for doubting that the bird in the trap was the individual that had laid it. Dr. J. P. Chapin, to whom Sabater sent both the egg and the pickled corpse of the bird, informs me that the egg measures 21.6 by 17.7 mm. These dimensions agree well with the known eggs of the closely related *Indicator variegatus*, and this agreement strengthens the validity of the identification. The exact locality of Sabater's specimen is a forest patch called Afán Otóng Nguíng, near N'Koumadjap, Spanish Guinea. Another female, taken at the same time, was also in breeding condition. Its ovary contained one ovum about 9 mm. in diameter and 10 or 12 ova about 1 mm. each in diameter.

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[17] *Indicator stictithorax* Reichenow, Journ. Ornith., vol. 25, p. 110, 1877. (Cameroons.)

No other eggs and no nestlings of this bird have yet been found. There is no reason for assuming that its breeding habits will prove to be different from those of *I. variegatus*, but we have nothing to go on. Williams (1951, p. 108), who collected the breeding male in the Bwamba forest, western Uganda, refers to the fact that nearby was a colony of brown barbets, *Gymnobucco bonapartei*, "which may have acted as hosts to the honey-guide." Bates (1930, p. 269) suggests a possible adaptive similarity in coloration between this honey-guide and one of the woodpeckers, *Campethera nivosa*, a mimicry which, if actual, would suggest that the latter may be a regular host of the parasite.

At Ntandi, in the Bwamba forest, the van Somerens (1949, p. 43) watched one of these honey-guides inspecting a barbet's nesting hole within a few feet of where they were sitting. "It alighted below the hole, entered, came out, and re-entered. When it emerged within a minute or so, it sat on a nearby branch as though hesitating or contemplating a further inspection. There were no eggs in the hole."

Songs and Calls

In the Bwamba forest, Uganda, Williams heard this bird give a curious call, a low purring *brrrrr* repeated at intervals of a minute or so, a song that is evidently not very unlike the purring or croaking call of the male of *Indicator variegatus*. Williams' experience with it closely parallels my own with the latter species. It took quite some time before he could see the calling bird, which was sitting on a branch of a tall forest tree, and every time it produced its guttural purring it puffed out all its feathers, making it appear much larger momentarily, and then resumed its hunched-up posture.

The bird Williams watched proved, on collection, to be a male in breeding condition. In the same forest the van Somerens (1949, p. 43) saw several individuals which were silent, causing them to comment on "a marked absence of any call notes such as we have noted for *I. variegatus*." It may be that this purring sound is given only by the male during the breeding season.

In the Cameroons, Bates (1909a, p. 15) reports that his native assistants told him that this honey-guide gives a cheeping cry, *woé, woé* (woé being the native word for honey). Whether this is something read into the call is not known.

Food and Feeding

In its food habits this species is essentially similar to *I. variegatus*, feeding on beeswax, bee larvae, and other insect prey. In the Cameroons, Bates (1909a, p. 15) found particles of wax and bits of insect remains in the gizzards of four specimens. There was a smell of honey in these stomach contents, but in some there were only insect remains. J. P. Chapin (1939, pp. 547–548) reported insect remains in the gizzards of two birds from Gamangui, and also some sand in one of them. A third bird, taken near Beni, had beeswax mixed with bits of insects in its stomach. The stomach contents of this individual, examined later for me by Dr. E. A. Chapin, proved to contain remains of parts of three small ants, one large ant, two bees, two large spiders, one small spider, one termite, and one caterpillar. The specimens from Gamangui were trapped in heavy forest by natives in snares close to the ground and baited with fragments of termite nests. That the birds often come down close to the ground to feed is further indicated by the van Somerens' observations in the Bwamba forest, where they noted them "hunting for insects at quite low elevations." In the gizzard of a specimen collected there by Williams were numerous insect remains, including lepidopterous larvae and fragments of beetles, but no wax. In the Cameroons, Bates noted these birds perching "silently watching the bees buzzing about the camp, for bees are attracted to fresh clearings in the forest." An adult female from Spanish Guinea, collected by Sabater, had in its gizzard two species of ants, a quantity of termites, one unidentified seed, and some beeswax.

This species does not guide humans to bees' nests, and it is not known whether it acts in this capacity for any other creatures—squirrels, monkeys, etc. As Bates puts it, in the Cameroons the natives told him that "sometimes on going to where the bird is they find honey but they know nothing about following the bird through the forest."

Miscellaneous

Like other species of *Indicator*, *maculatus* has a very tough, strong skin. Bates (1909a, p. 116) writes that the skin "like strong yellow parchment and the thick layer of fat are doubtless protection against the stings of bees." I know nothing of this bird from personal experience, but I have never seen any conspicuous layer of fat on any of the other species and cannot help but wonder if *maculatus* does have such a characteristic regularly. Chapin (1939, pp. 547–548) noted that his specimens emitted a peculiar musty odor before being skinned, and that this odor adhered to the compact plumage after the skins were made up. This odor is said to be found in other honey-guides as well, but I have never noted it in *I. indicator*, *I. minor*, or *Prodotiscus regulus*, the species I have handled in the flesh, or in other species in museum collections.

Description

Indicator maculatus stictithorax

Adult (sexes alike in coloration): Forehead, lores, crown, occiput, and nape olive to dark greenish olive, some of the feathers of the anterior part of crown and forehead with narrow edges of ecru olive to light yellowish olive; entire upperparts of body and wings bright dark citrine with a yellowish green wash, the bases and concealed median portions of the feathers dull, dark clove brown to fuscous; remiges fuscous, externally edged with bright citrine, these margins broader on the secondaries than on the primaries, and not reaching the terminal part of the primaries, the remiges margined internally for most of their length, except terminally, with creamy white; median two pairs of rectrices dark clove brown to fuscous, edged with citrine; the other rectrices white with broad dull olive brown tips, these dusky areas extending farther down on the outer than on the inner webs, this becoming more extensive as a lateroterminal edging on the outermost pair; lores, cheeks, and auriculars dull brownish olive, the feathers of lores and lower cheeks in some specimens with narrow whitish edges; feathers of chin and throat streaked, with dull, dark olive shaft-stripes and fairly wide whitish margins, breast feathers citrine with one latero-terminal round spot and one subterminal one of yellowish white on each web; on feathers of upper abdomen these lateral spots tend to elongate and to become slightly darker—creamy buff to Naples yellow with a light olive wash; rest of abdomen with the lateral spots fused to form broad edges to the feathers, the citrine being restricted to the shaft stripe which becomes increasingly narrower posteriorly, the lower abdomen and vent being largely pale cream or buffy with yellowish green tinge; feathers of flanks and thighs with broad median stripes of dark olive to dark citrine, edged with cream or pale buff; under tail-coverts similar but with the dusky shaft-stripes narrower; under wing-coverts cream to almost white with some indistinct grayish markings; iris dark brown to brownish ochre, bill blackish, the base of the mandible greenish brown to pinkish brown; feet dark green. Measurements of males, in millimeters: wing 97–111, tail 59–73, culmen from base 14.6–15, tarsus 15–17.5; of females: wing 99–103, tail 59–63, culmen from base 14–14.3, tarsus 16–18.

Juvenal: Similar to the adult on the upperparts except that the basal and median portions of the feathers of the crown and occiput are slightly darker (dark fuscous), the general greenish tone of the back and wings slightly less yellowish (dark citrine); below darker and more conspicuously and abundantly spotted with creamy to pale buffy white; chin and upper throat with the dusky median portion of the feathers broader and branching laterally to cut up the pale, whitish margins into spots; ground color of the feathers of the breast, upper abdomen, and sides dark greenish olive, causing the pale spots to appear, by virtue of the greater contrast in color, more conspicuous than in the adult; broad median portion of flank feathers and of under tail-coverts somewhat darker than in adults; rectrices more pointed; under wing-coverts as in adults but with fairly definite, but subdued, transverse markings; axillars white barred with dusky citrine.

Natal down: Unknown, if any.

Indicator maculatus maculatus

The nominate race of Upper Guinea, *I. m. maculatus,* differs from *I. m. stictithorax* in being somewhat duskier on the crown and occiput, in having the feathers of the cheeks and malar region uniform dark olive with no whitish margins, the abdomen less washed with yellowish, and the pale breast spots not quite as distinct from the ground color of the feathers.

Variegated, or Scaly-Throated, Honey-Guide

Indicator variegatus Lesson [18]

Figures 1, 2,*b*, 3,*a*; Plates 6,a, 12, 21

Distribution

Ecological range: In my personal experience the variegated honey-guide was much more of a wooded-river-bottom dweller than either the greater or the lesser honey-guide. In the Umtaleni Valley, eastern Cape Province, I never saw it except in the forest along the stream, while the other two local species of the genus were chiefly in the drier, more open hillsides, although both came down into the woods as well. Nevertheless, it is obvious from the literature and from the notes of other observers that *I. variegatus* actually has as wide an ecological range as *I. indicator.* Thus Jackson (1938, p. 734) found this species to have a marked partiality for the bushveld, "and this is very noticeable in Uganda, as they are rarely seen or heard in places . . . within twenty miles of the lake." J. G. Williams writes me that in his experience with the species in Kenya Colony it is widespread but everywhere uncommon, frequenting open bush and savannah country and generally avoiding the thickly wooded and forested areas, although it is sometimes found on the outskirts of forests and along wooded riverbanks. It also occurs in very dry bush country, as indicated by a specimen from the Garissa district. Meinertzhagen (1937, p. 745) found it as high as 10,000 feet in the bamboo zone on Mount Kenya. In the Sudan, McDonald and Cave (1948, p. 245) record it up to 10,000 feet as well, and on Mount Elgon it is said to occur up to 11,000 feet (Chapin, 1939, p. 546), but it is chiefly a bird of lower country.

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[18] *Indicator variegatus* Lesson, Traité d'ornithologie, vol. 2, p. 155, 1830. (Africa.)

In the Belgian Congo it is recorded only east and south of the great forest—near Kasindi, in the upper Semliki Valley, Mahagi, Nshiri, Nkungu, Akanyaru River, Kasaji, at Lukafu in the Katanga, at Katapena to the south of Lake Upemba, and in southern Marungu (Kinia and Kampia), and at Mulungu, very near the eastern edge of the great forest—inside of which it is replaced by the closely allied *Indicator maculatus*.

In Tanganyika Territory, Moreau considered it a denizen of the tree tops in the evergreen forest community of the Usambara Mountains. In Nyasaland, Benson (1940, p. 429) recorded it from 2,300 to 6,000 feet in evergreen forest, in tall luxuriant *Brachystegia* woodland, and in stream-side scrub; he (Benson, 1953, p. 45) also reported it once in an *Acacia albida* tree in a cultivated area. In Northern Rhodesia, White (1946, p. 73) observed it at the edges of the evergreen forest. Similarly, in Southern Rhodesia, Irwin (1953, p. 40) considers it more or less confined to the eastern parts of the country, where patches of evergreen forest occur with some frequency. Roberts records it chiefly from the southern forested areas of South Africa, east and southeast in the low veldt. In Mozambique, Rosa Pinto (1953, p. 40) obtained specimens at Lourenço Marques, Goba, and Coguno, but he gives no details as to the type of habitat.

Geographical range: The range of the variegated honey-guide extends from the southeastern Anglo-Egyptian Sudan (Lotti forest, Imatong, Dongotona and in the Didinga Mountains up to 10,000 feet), south-central Ethiopia (Uanda, Goba, Gardula, Uba), and southern Italian Somaliland (Dogge, Anole, Heleschid, Jonte, Ola Uager, Alto Bubasci, Juba River, etc.), southwards across the eastern Belgian Congo east of the great forest, Uganda, and Kenya Colony, across Tanganyika Territory, Mozambique, Nyasaland, the Katanga, Angola, Northern and Southern Rhodesia to the Transvaal, Natal, and the eastern Cape Province, west as far as the Uitenhage area.

In this whole area *Indicator variegatus* is rather local and appears to be less numerous than either *I. indicator* or *I. minor*. It is divided into two subspecies, the ranges of which are as follows:

I. v. variegatus: Southeastern Anglo-Egyptian Sudan and south-central Ethiopia, south through eastern Belgian Congo, Uganda, and the interior of Kenya Colony (all but the lowland coastal and subcoastal belt), to Tanganyika Territory chiefly west of the Rift Valley (not on Kilimanjaro and the Usambara Mountains), the Katanga, Angola, the Rhodesias, Mozambique, and South Africa.

I. v. virescens: [19] Southern Italian Somaliland, coastal Kenya Colony (Sokoke, Malindi, Rabai, Ualimi, Tana River), and eastern Tanganyika Territory (Kilimanjaro area, Usambara Mountains, Useguha, Uvidunda Mountains, Lindi (?)). It is possible that the birds of eastern Mozambique may yet prove to belong in this race rather than in the nominate one.

Breeding Range and Season

The scaly-throated honey-guide undoubtedly breeds throughout its very extensive range, but actual data are scanty. Below are listed all bits of evidence known to me.

South Africa: Isipingo, Natal, October 29, egg record; Woodbush, Transvaal, December 3, egg record.

Southern Rhodesia: Banket, November and early December, eggs.

Nyasaland: Mlanje, April 24, adult male, gonads indicating "at end of breeding season"; 70 miles south of Fort Hill, October 24, adult male with testes somewhat enlarged; "breeding, August to October" (Mackworth-Praed and Grant, 1952, p. 741).

Mozambique: Namuli, August 2, 3, adult females in breeding condition.

Tanganyika Territory: Amani, Usambara Mountains, fledgling observed; no date.

Kenya Colony: Kidong Valley, May 21, egg; Ngong, July, nestling; coastal belt, June, nestling; west of Lake Magadi, South Uaso Nyiro River, May–June, fledgling.

Uganda: February and May, nestlings; Mubendi, September, adult male in breeding condition.

Belgian Congo: Kenia, Upemba Park, July 15, male in breeding condition.

Songs and Calls

The usual "song" of the scaly-throated honey-guide, given regularly at the call posts by adult birds (it is not yet known if this note is given only by the males or if the females may also give it) is a low, rather gutteral purring, or almost croaking, froglike note that may be written *ghrrrr.* It lasts about 2 or 3 seconds and is given at intervals from 1 to 1½ minutes. When about to start its call the bird arches its neck slightly, getting its head into a somewhat more horizontal position than it ordinarily has, ruffles the throat feathers slightly, and then calls. As it produces the sound, its body and tail feathers quiver slightly. In the Umtaleni Valley, eastern Cape Province, Ranger introduced me to this bird and I spent many hours watching it at fairly close range. Its croaking or purring note is one that would easily be unnoticed as it is quite unavian in quality, and might readily be assumed by a passing naturalist to be of insect or amphibian origin.

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[19] [*Indicator variegatus*] var. *virescens* Reichenow, Journ. Ornith., vol. 17, p. 274, 1889. (Lewa, Usambara, East Africa.)

The hours of song utterance are greater in this species than in either the greater or the lesser honey-guide. The earliest that I ever heard the bird call was at 5:45 a. m., but the following year Ranger recorded the croaking song as early as 4:39 a. m., before daybreak. One morning I kept an accurate count of the song delivery of a bird at a call site and found that from 6:50 a. m. until 8:20 a. m., when I left, the bird gave its call some 76 times. On another day Ranger and I went to the call site at 9:35 a. m. and neither saw nor heard the bird, but 10 minutes later it flew in from a secondary post, completely silent. As I approached it, it flew back to the secondary post, and called from there at intervals of exactly 1 minute (by watch) until 10 a. m. when it returned to its main call post and began calling from there at 10:01 a. m. It kept up calling at 1-minute intervals until we left at 11:30. The bird was apparently not interested in us, in feeding, or in anything else, but merely sat on the same spot and reiterated its monotonous purring. When "singing" the bird usually seemed to choose the higher branches under the canopy of the tree. In the afternoon I have noted the bird calling only from about 3 to 4:05 p. m., but it is not restricted to these limits, as Ranger recorded it as late as 7:10 p. m. in his 1951 field notes. He and Skead had been watching a bird giving its whistle-calls (not the call-site "song") as it worked its way along in a wooded kloof, and at 6:50 p. m. were astonished to hear the call-site call. "It was heard again and again subsequently as the bird worked its way down-stream, the last being heard at 7:10 p. m. The sun had been down for some time when the whistling and croaking were heard. We now have records of this call well away from the call sites and at a late hour. We also know that they (the birds) move about a very great deal."

In the summer of 1951 Ranger watched two supposedly male *variegatus* with call sites about 280 yards apart and found that the song of each bird was audible at the site of the other. If the sound was detectable to the human ear it probably was to the birds as well. In Ranger's experience this croaking or purring "song" is given practically throughout the year, with a marked decline in late summer—late January to mid-April. In the summer of 1952 Ranger noted a great range of variation in the purring call-site note, from the low, froglike croaking described earlier to a loud vibrant rolling note with something of the quality of a policeman's whistle in it. What appears to have been this type of note has been described by several authors: the Woodwards (1899, p. 107) in Natal, Woosnam (in Ogilvie-Grant, 1910, p. 414) in Uganda, Benson (1937, p. 560; 1940, p. 429; 1942, p. 299) in Nyasaland as a trill or a deep trilled whistle lasting occasionally even 3 or 4 seconds and (1948, p. 55) ascending the scale a full octave. In none of these published notes is there any indication of the meaning or function of this type of vocalism.

In the eastern Cape Province, Ranger and Skead watched a male (?) scaly-throated honey-guide giving its croaking, purring song from its call post when another individual came close to it, whereupon the first bird broke off its croaking song in the middle and chased the intruder in a most determined fashion, swaying, swerving, and with direct, not undulating, flight. "As the two birds flew off, we heard a call new to us, a series of annoyed and husky *kizz, kizz, kizz,* very similar to the call we had heard *I. minor* make during its chase this morning and also to the noise made by *I. indicator* after copulation. Soon a bird returned to V1 (the call site) and resumed calling. Although the inference that the intruder was *variegatus* is strong, and in our opinion very probable, that action was so quick that identification was impossible. It might have been a wandering *I. indicator.* We have twice seen the species amicable at a bees' nest but at call sites they may be different. When we left both birds were calling at V1 and V2 (two call sites of *I. variegatus* about 250 yards apart)."

Other notes described in the literature are as follows. Meinertzhagen (1937, p. 745) heard a *ka, ka, ka* note repeated by guiding birds. This is apparently an alternative rendition of Ivy's (1901, p. 21) *cha-cha-cha.* Priest (1934, p. 508) records a harsh and persistent *charr-charr-charr* often repeated. Williams writes me that in his experience with it in Kenya Colony and Uganda the bird is usually silent, but at times produces a chattering call note. All of these descriptions probably refer to the same type of vocal utterance. Van Someren (in Mackworth-Praed and Grant, 1952, p. 741) records a long drawn out *cheee-tii, cheee-tii.*

Moreau (in Sclater and Moreau, 1932, p. 665) kept in captivity for a few days a scaly-throated honey-guide that had stunned itself against a window and he heard only a squawk note from it.

Roberts (1940, p. 187) describes the call notes given from the treetops as a "pretty, not very loud whistling in a high key." Aside from the lack of meaning in such a word as "pretty," I cannot reconcile this description with any other known call, unless it be the following (the data on which are entirely the observations in the eastern Cape

Province by Gordon A. Ranger, to whom I am indebted for them). This call is a series of rather ringing, mellow, and plaintive whistled notes, varying in number from 1 or 2 to 6, with an interval of a few seconds between the series. The notes may be written *foyt-foyt-foyt*, with the interval between them about half a second. It is uttered both in the morning and in the afternoon. Ranger had known this call for a number of years, but was unable to attribute it with certainty to *Indicator variegatus* or to the commoner species, *Indicator indicator*. On July 8, 1951, he heard the call nearby in the streamside forest, and then heard it repeated, whereupon he imitated the sound. Immediately a scaly-throated honey-guide came and perched so close to him that it was out of focus in his binoculars. As it moved off a little he was able to satisfy himself of its identity. To quote from his letter:

> The bird was so interested and responsive to my whistle-imitation after this that I kept it flying about me. Another bird, which I thought to be *I. indicator*, appeared and chased it off two or three times, but it returned each time in response to my call. . . . *Variegatus* uttered incomplete calls during this play and specially when out of my sight, and then my imitation brought it back to me.
>
> Now, when I walked on in the forest the bird accompanied me, first at my whistling its call as I went, and then apparently purely through interest in myself who had uttered the imitation. It went ahead of me—not in my line, but in a parallel line about 30 yards from mine—uttering its call at times. I imitated it and when I ceased to do so it still followed. When I emerged from the forest edge it followed, not called by me, keeping in the edge [of the forest] below me and ascending a narrow ravine-arm which I crossed ahead of it. As I diverged from the line of this ravine the bird flew out toward me a little in ascending the ravine, calling, and continuing to call when it reached the furthermost point where it perched in view low down. As it appeared disposed not to follow me over the grass hillslope I called repeatedly as I withdrew but it did not follow . . . The distance it followed and accompanied me is about 300 yards.

A week later, with the new knowledge outlined above, Ranger went to the favored call site where he had listened to the bird giving its purring "song" for many years.

> At 30 paces from the bird and out of its sight, I sat down and imitated the whistle call. Almost immediately the site bird flew from its post directly to me and alighted 12 feet from me and 7 feet above the ground. It was wide awake in attitude and after a few seconds uttered its site call (purring note), and, after the usual interval, a second time. Then, turning my face away from the bird, I whistled the imitation of the whistle-call three times with proper interval. The bird's reaction was to peer very intently among the surrounding trees, but then it seemed to satisfy itself that a fellow bird was not present and flew back to its call post and resumed calling (*i. e.*, giving the purring note). Now, when I repeated the whistle call, it came only half way toward me, and further tempting by me was unavailing. It flew back to its site post when I moved toward it and continued its calling. Two more attempts to induce it to investigate my whistle-calling uttered from other and more distant quarters proved fruitless. The bird took no further notice and proceeded with its call-site calling. The question 'why did this bird disregard my further attempts to attract it,' is asked . . . Is

the all-important recognition factor the sight of and movement of the other bird itself? Its behaviour did illustrate, however, how real and fixed and important the call site is.

With the object of attracting *I. variegatus* I uttered the whistle-call wherever I went in the forest this day. With this intent I entered the lower end of the forest dale in which I met the bird on 8 July, uttering the call as I walked up the stream. I had not gone more than 100 yards when a bird appeared, perching over the stream bed. As I advanced it made way but followed me again after I had gone ahead and called it. In responding to my . . . whistle . . . it would fly past and ahead of me and settle; and as I approached would move away at right angles to my line of progress. Then on my calling ahead, it would reappear flying past and above me. In this way it followed me to the top of the forest dale. At no time did it utter a sound. Within the top of the forest dale I sat down to call the bird who was not in sight. It came and perched near; and for the first time uttered only two or three notes of its call. Now when I walked away in departure, calling, it failed to follow. That ended the occasion. Twice I tried the experiment of not calling after I had walked ahead up the stream, sitting down to wait for it, but it failed to follow, doing so only when I called. Distance this bird followed me is about 400 yards.

It did not appear to me that the bird was leading me on in the forest on 8 July when it went ahead. Nothing suggested that there was the least shade of 'guiding' . . . It is not my purpose to convey that idea. The occurrences are related as they happened. But is it possible that my behaviour and myself awakened or set in motion some degree of instinctive response in the bird—response related to what we call 'guiding' in *I. indicator*? Or is the bird's interest merely curiosity in the object with which, or in whom, its call is associated?

More recently Ranger (in litt., October 1952) described many additional observations and summarized his experience as follows. It appears that the bird maintained an interest of some kind in him as long as he was the source of the whistle-calling, or in face of his repeated whistle-calling, but there were many times when the bird, sensing that these calls came from him and not from another honey-guide, immediately lost interest in him and then disregarded his subsequent whistle-calls. At the same time the fact remains that the only way he was able to engage the attention or interest of the bird was by making the whistle-call, either in response to a bird heard to make it, or initially to cause the bird to respond. The bird was never known to initiate any demonstration of interest in him as another animal in the way *Indicator indicator* often does. It is also apparent that *Indicator variegatus* shows no selection that may even remotely be called intelligent in its reactions to the human and the whistle-call. Ordinarily the whistle-call is uttered by birds on the move, or by birds going from one part of their range to another, with the result that the individual notes of a series of five or six notes each are spaced by distance as well as by time. There is evidence that this call is sometimes given by call-site males (?) when leaving the call site, and also when coming to it.

Another note, recently studied by Ranger, is one that may be termed a "protest note" directed by an established call-site bird against intruders of its own kind in the vicinity of its call site, or by an intruder attempting to take possession of the area. This note, described more fully in our discussion of courtship and mating, is an inflected trill, *trrreeephew.*

Still another type of vocalism has recently been observed by Ranger (in litt., October 1952). This note suggests the nature of the sound produced by passing the thumbnail over the teeth of a comb. On one occasion it was also combined with a trill composed of the notes of the whistle-call.

Courtship and Mating

There are no data on the courtship and mating behavior of the scaly-throated honey-guide in the literature. In my effort to assemble additional unpublished information I corresponded with the majority of serious observers of African birds and none of them had the slightest bit of information to offer, with the sole exception of Gordon A. Ranger, who not only introduced me to the species in the field but enabled me to see for myself that the call-post behavior present in *Indicator indicator* and *I. minor* was also present in this species. However, even Ranger, with all his years of field acquaintance with the bird, had never seen any sign of either courtship or mating. Considering the countless hours that Ranger has spent watching the species, as well as the much briefer but intensive application to it by Skead, Pringle, and myself in Ranger's company, it seems safe to conclude that courtship posturing must be rarely indulged in, if at all. This is not surprising when one recalls how very few notes could be brought together on courtship in the much better known *Indicator indicator.* Honey-guides seem to be largely devoid of such behavior.

My own observations of the call-site or call-post behavior were made in November 1950 in the Umtaleni Valley with Ranger, Skead, and Pringle. Here one bird, presumably a male, was watched day after day for hours at a time. Its "singing" area comprised four different trees, three of which were on one side of a stream, one on the other. The stream was about 18 yards wide; all four of the call posts could be included in a triangle with a base of about 35 yards and a height of 31 yards; the area involved being noticeably smaller than that for either *I. indicator* or *I. minor.* Unlike these congeners the bird showed no predilection for a favorite twig in each of its call-trees as long as it was high up under the canopy. This call site was known to Ranger as held by *I. variegatus* continuously since 1925 (26 years)!

Ranger is the only naturalist to have published on the tendency of the variegated honey-guide to call persistently from a given tree, and his very brief note, printed in the Blythswood Review, February 1932, failed to arouse the attention it deserved, partly because of the limited circulation of that periodical. The additional bits of information recorded below are likewise due to Ranger's continued observations.

A mounted female scaly-throated honey-guide, supplied by the Kaffrarian Museum, was sent to Ranger who placed it in a favorite call-site tree of *I. variegatus.* The live bird (male ?) returned soon afterwards, perched not more than 2½ feet from the mount, and began to give its purring song in perfectly normal fashion. No reaction whatever to the mounted bird could be detected. Apparently the dead mount was nothing more significant than another twig or some inanimate object in the immediate scenery to the live bird, which, in the course of 10 or 15 minutes, used two other perches within 5 feet of the mount and so was in a position to see it from all sides. When one recalls the relative ease with which it is possible to get male birds of many species to display and even to attempt copulation with mounted hens of their own kind, or to drive away mounted males, it seems more likely that the honey-guide recognized the mount as one of its own kind but showed no interest in it, rather than that it did not even recognize it. Since the sexes are alike in appearance, this might seem to suggest a lack of exclusiveness or other indication of "rivalry" or "jealousy" between males at a call site, similar to the situation existing in *I. indicator.*

However, subsequent observations by Ranger (in litt., November 1951) reveals that "the calling male at the site does decidedly demonstrate jealousy [chasing away other birds] and uttering a sound of remonstrance each time he returned to his call post, and on the appearance of the other bird . . . This holding the site jealously complicates matters: the facts at *I. indicator* site suggest the absence of 'jealousy.' Also, how does another bird take over calling at the site when jealousy holds sway? In each of these cases I called one whistle-call at or near the one site and this brought the other, or the chased birds, to it. Chasing on November 25 lasted 8 minutes; but on November 4 it was a shorter affair." Still further observations by Ranger and Skead are of interest in shedding more light on this subject. It must be emphasized that the interpretation of the trilling sound as a sort of protest against intruders of its own species in the vicinity of a call site is only a tentative one, although probably correct, for the reactions of the birds are not always uniform. Ranger found that by imitating the whistle-note of the scaly-throated honey-guide he could get the singing male to leave the call site and come to him with this "protesting" note. Once Ranger was seated between two known call sites, 250 yards apart, on each of which the male birds were heard calling at the time. He imitated the whistle-call for a few minutes and then a scaly-throated honey-guide flew over him, and veered off into the bush just before reaching the call site of the other bird. For about 30 seconds there was silence and then a bird appeared from the second call site and settled in a tree about 30 yards away. As the intruder from the first call site sat there the bird from the second site gave three bursts of the protest utterance, *trrreeee-phew.* Ranger's experience has been that on the occasions when he has whistle-called and two birds have been seen near each other at the call site this "protest" call has resulted. When only one bird was found away from a call site it responded with the whistle-call, not with the trill of protest. This trill is high-pitched, quite rapid, and with a noticeable inflection.

Still more recently (October 1952) Ranger sent me some highly interesting observations concerning one bird (presumably a male) taking over the call site from its former occupant. Fortunately, the two individuals were readily distinguished in the field, as one, the original occupant and the defender of the site, was in the process of molting its tail feathers and had an assymetrical, "untidy" tail, while the newcomer had its complete complement of fully grown rectrices. For the purposes of easy reference the former bird may be called M (for molt), and the latter C (complete).

At 11:05 a. m. on March 30, 1952, as Ranger walked up to the immediate area of the chief call site of M, a variegated honey-guide flew from a tree a few yards from the central calling trees, circled about them, and lit on the favorite one. From here now came the most urgent protest crying yet heard from this species—the protest note made into a shriek. After a little while this calmed down to the ordinary protest note (without the terminal *pheeuw*), and this, in turn, was followed by the urgent crying of two birds and their chasing flight around the site, and then by their perching near each other, still excitedly giving the protest shrieks. This activity lasted 7 minutes in all, and ended with the birds alighting near and above Ranger, perching about two feet apart on different levels. Here they sat still and silently regarded each other in apparently tense, alert fashion, only their heads moving at times in a very slow manner to direct a stare at each other, one of the birds blinking frequently with both its eyelids and its nictitating membrane. For 33 minutes this silent sitting went on, and at 11:45 the birds suddenly darted off in flight, in close chase. Owing to the fact that Ranger had his glasses trained on only one of them at that instant, it could not be determined whether M or C initiated this chasing flight. The two birds settled again, M continued giving the protest notes for 5 minutes while C remained silent; then a renewal of the chasing, and then C gave the guttural, purring site call (i. e. the "song" given by an established bird at its call site), and M repaired to the central site to utter the protest call. For the next 15 minutes M kept shrieking its protest notes, then 2 minutes of silent moving about in the tree, then protest calling from both birds near together. This was followed by about 2 minutes of silent sitting, the birds quietly watching each other at very close range, then again both began to give their protest calls, and again a period of silent sitting just outside the central call site. At 12:09 they flew 20 yards upstream, first shrieking, then silent; at 12:14 they flew back to just outside the central call site where both began to shriek profusely. After a short break in this noise, C gave the purring site call, whereupon M approached C crying its protest notes but then returned to the site proper, still crying. More of this alternate calling, silent sitting, and chasing for another 15 minutes. At 12:53 C darted up and out (or at?) M, who also rose up suddenly (almost simultaneously) and they flew off in chasing flight, C close behind M. During this pursuit one of the birds was heard to utter a little chattering crying similar to that given by *I. indicator* at the site during sexual pursuit, and also similar to that occasionally made by *I. minor*, a series of *kizz, kizz, kizz* notes. At 1:09 the demonstration was still continuing; C again gave the purring site call, and M cried its protest and was alertly watching C; then M also gave the site call, which was, however, very weak and subdued, or hushed. C again gave the site call and M dashed off in its direction shrieking a great deal as it went. Then followed much chasing with M close behind C, both shrieking protest notes excitedly until 1:26, when Ranger left.

Throughout, M did far more "protest" crying than C, and showed itself to be the individual defending the call site, which it "held," launching its attacks on C from it, and coming back to hold it in an alert look-out manner, and issuing forth again after C had indicated its persisting presence by giving the site call from one or another of the outer limits of the call site. C usually was not allowed to perch at the central site, and all its purring "songs" were given from the outer points of the site. Two of the long "silent" sittings did take place at the central site, however. Ranger writes that it is difficult to describe the "method" in the behavior of C, but it was a kind of passive, patient persistence. "The bird did stand up to M on equal footing with it during the spasms of protest shrieking and during the several silent perchings . . . The icy tenseness of the silent slow-gazing sitting was relieved by a chasing initiated by one or the other. The longest silent sitting lasted 33 minutes. The average was of course very much shorter—a few minutes. When shrieking at each other the attitude of protest or defiance in the birds was enhanced by the wide open gape with the lower mandible vibrating up and down very rapidly." The next day Ranger revisited the call site and found M and C still repeating the above behavior. However, on the following day and the next, only C was to be seen at the call site, and giving the normal guttural, purring "song."

In this connection, another recent discovery by Ranger may be described, a display reaction apparently relative to the appearance of another individual. This he observed twice, on August 24 and September 9. When he gave the whistle-call in response to that made by the bird, it came into view about 15 yards off in a flitting, hovering manner, rising up to a perch.

> The movement is a fluttering, halting hovering which begins on a lower level than the perch the bird eventually takes up, and about 6 feet from it. The attitude of the bird is similar to that of a nectar-feeding bird hovering before a flower . . . I am under the impression that the birds uttered the whistle-call during the hovering movement but am not certain on this point . . . The whistle-call, however, was made from the perch upon the bird's alighting there from the hovering rise, and the protest trill as well in the case of September 9. This hovering movement is not a stationary hovering before the perch, but a hovering progression to the perch.

Corroborative observations of call-post behavior in this species come to me from Darrell C. H. Plowes (in litt.). In July, at Mtunzuni in the coastal belt of Zululand, he and a friend watched a male (?) variegated honey-guide calling from a certain tree for quite a long time, and his friend informed him that the bird was to be heard calling from that tree at almost all times of the year. A few days later Plowes found another similar instance in the Ngoye forest.

Seasonal Movements and Site Tenacity

The scaly-throated honey-guide is nonmigratory and has been the subject of so little observation (and that little so casual) everywhere except in the Umtaleni Valley that the published records of birds seen or collected give no information as to any local wanderings. Ranger's observations show definitely that singing birds (presumably males) have definite call sites from which they give their curious croaking song hour after hour, day after day, for months on end, in fact, almost throughout the year. He has known of three such sites that have been in fairly regular occupancy by this species from 1925 to 1952, and one of which, definitely known to be used since 1942, still is in use at the time of present writing. This suggests site tenacity, at least on the part of the singing males, but we have still to determine the extent to which the same individual clings to the call post, and whether the "stud post" behavior described for *I. indicator* actually occurs in this species as well. The implications are that the picture here is probably essentially similar to that in *I. indicator*, although differing from the latter in that *I. variegatus* has a "protest note" used against intruders of its own kind at the call site; or, in other words, that *variegatus* shows some sign of "exclusiveness" or "jealousy" in its call-post occupancy, while *indicator* does not.

Notes made by Ranger and Skead in 1951 reveal that these honey-guides move about a great deal, but usually do not give their croaking or purring notes except from definite call sites. Skead (in litt.) summarizes his findings as follows: These birds roam a great deal and are very rapid fliers; "obvious honey-guides" dashing up and down stream in a wooded kloof at all times of the day made it apparent that they cover considerable ground, although there were no data then suggesting that the birds go more than a few hundred yards from their call sites. However, birds apparently established on their call sites did leave them for considerable periods of time, in which they could have gone much farther afield. Apparently this species does not adhere as closely to its call posts during the day as does *Indicator indicator.* On one occasion Ranger saw one about a mile from the one known call site, and another 1,100 yards beyond this again, but there is no proof that these observations pertain to the bird or birds using the known call post. The extent of the wanderings of an individual bird is suggested by the following recent note of Ranger's: A banded bird originally trapped at a wild bees' nest on June 17 was retaken at the same spot on July 19 and again at another bees' nest three miles away on August 24.

EGGS AND EGG LAYING

The eggs of the scaly-throated honey-guide are not certainly distinguishable from those of the lesser honey-guide, but appear to average slightly wider in proportion to the length than those of the latter species. There is, unfortunately, but a single completely authenticated egg of *I. variegatus* known. This one is reported by Neuby-Varty (1948, p. 158), who took an egg ready to be laid from the oviduct of a female shot on November 24, 1947, on the Umvukwe Ranch, Banket, Southern Rhodesia. It was glossy white and measured 20.75 by 16.5 mm. Another egg also was taken by Neuby-Varty (1946, pp. 345–346), who watched a pair of black-collared barbets trying to keep a scaly-throated honey-guide away from their nest. He says—

> . . . as I wanted the honeyguide's egg I climbed up and in removing a piece of bark about 1 inch square from the back of the nest I noticed I was through to the nest and could remove the egg that was there, which I did, but as it looked like a barbet's egg I put it back and replaced the bit of bark. By this time all three birds were not to be seen. I climbed down . . . and watched. I had been about 5 minutes in my hide when out of a tree about 30 yards away the honeyguide came out, flying very fast. It flew straight into the nest, not even hesitating at the entrance, and in three seconds it was out and flew away. I waited for another

> ten minutes and as it did not return climbed up and removed the piece of bark and to my surprise there were two eggs.

Unfortunately both eggs were broken when the collector fell from the tree as the branch gave way under him. Some time later he found another pair of the barbets also trying to keep a scaly-throated honey-guide away from their nest. Three days later he opened the nest and found it contained six eggs, four of which were black-collared barbet's and two were honey-guide's eggs, attributed to *I. variegatus*, "white, very glossy, oval in shape, measuring 21.72 mm. X 16.5 mm. and 20 mm. X 16.5 mm."

The above observations yield the following data: The scaly-throated honey-guide did not remove an egg of the host when laying its own, and the total time spent by the laying bird in the nest of its victim was very short—three seconds from the time it entered until it left. Mr. Neuby-Varty further informs me that this particular instance of egg laying took place between 9 and 9:30 a. m.

Eggs attributed to this honey-guide measure 20–21.7 by 15.4–17 mm., compared with 20.3–22.6 by 14.5–17.9 mm. for *I. minor* and 22.7–26 by 16.8–19.6 mm. for *I. indicator*. While those eggs included in the measurements for *I. variegatus* are ones whose attribution to that species seems well founded, it must be emphasized that the only completely authentic one measures 20.7 by 16.5 mm. as compared with a similarly indisputable oviduct egg of *I. minor* measuring 21.5 by 16.8 mm. As far as the admittedly meager material indicates, it seems that the scaly-throated honey-guide lays a relatively small egg for its size compared with either of the other two species here mentioned. In the case of the parasitic cuckoos of the genus *Cuculus*, small egg size has been looked upon as an adaptation to the egg size of their common victims or hosts, but it is not at all clear that this is the case here. Actually, in most cases (*Lybius torquatus*, *Trachyphonus vaillanti*, *Mesopicus griseocephalus*, *Campethera nubica*) the eggs of the host are larger than those of, or attributed to, the honey-guide, a condition of no apparent advantage to the parasite. It is possible, but not probable, that the absence of starlings from the list of hosts, if real and not due to paucity of data, may be correlated with the small size of the eggs of this honey-guide, which might tend to make starlings unsuitable to the parasite.

The eggs are laid only in nests in holes in trees or in banks; I know of no record of a scaly-throated honey-guide egg or chick in any other type of nest. As far as known, with one exception (and that one not a definite record), the eggs are laid in nests of birds that also lay pure white eggs. The apparent exception is *Petronia superciliaris*, the yellow-throated sparrow.

The few data available include but two records of more than one egg being deposited in any one nest. In these cases there is no certain way of telling if the multiple honey-guide eggs were laid by the same bird or not, but inasmuch as in one of those two cases one of the eggs was considerably longer than the other it would seem probable that two hens were involved. Contrasted with these two cases we have records of single honey-guide eggs in four other cases, as well as inferential single eggs in an additional four or five other nests. In no case is there any evidence of any pecking of the host's eggs. *Indicator variegatus* agrees in this respect with *I. minor* and not with *I. indicator.*

Nothing is known of the incubation period.

Hosts or Victims

Considering the enormous geographic extent and the great ecological variety of the range of the scaly-throated honey-guide, the known victims of its parasitism cannot be looked upon as anything more than the merest beginning of a definitive list of its hosts. Meager though the recorded data are, it may be noted that all of the known victims are hole-nesting birds. Of the 12 species of birds involved, 5 (1 with 3 subspecies) are woodpeckers, 4 are barbets, 1 is a swift, 1 a thrush, and 1 a weaver finch. Two of the barbets cannot be considered established definitely as hosts, while the records of another of the barbets, of 3 of the woodpeckers, the swift, the thrush, and the weaver finch all leave something to be desired in one way or another to make them completely certain. This leaves 1 barbet and 4 woodpeckers as the only birds unquestionably known to be victims of *Indicator variegatus.* The absence of records for any of the bee-eaters and starlings—common birds, many of whose nests have been found—suggests that in the choice of its victims this honey-guide is more like *I. minor* than *I. indicator.* (See accounts under each of these species, pp. 139–154, 192–204.)

Micropus horus (Heuglin). Horus swift.
Cypselus affinis var. *horus* Heuglin, Ornithologie Nordost-Afrika's . . . , vol. 1, p. 147, 1869. (Northeast Africa.)

One record.

The identification (by John G. Williams) of the honey-guide egg "almost certain," but admittedly by inference rather than by direct evidence. A. W. Vincent found a nest of this swift in the Kidong Valley, Kenya Colony, at the foot of the escarpment on the main Nairobi-Naivasha road on May 21, 1950, containing two eggs of the swift and one of the variegated honey-guide, the latter measuring 21 by 15.4 mm. The three eggs were in about the same stage of incubation, being very slightly set, with a little veining. The swifts, as is usual with this species, were nesting in a colony along a bank near a stream. The nest was in a chamber at the end of a straight passage about two feet long.

I am indebted to Mr. Vincent for writing me the details given above.

Stactolaema anchietae whytii **(Shelley).** Whyte's yellow-headed barbet.

Smilorhis whytii SHELLEY, Ibis, ser. 6, vol. 5, p. 11, pl. 1, 1893. (Zomba, Nyasaland.)

Two records, both uncertain as to the identification of the species of honey-guide.

In his report on Nyasaland eggs in the Belcher collection, Benson (1952, pp. 444, 445) writes that at Blantyre on October 16, 1921, two nests of Whyte's barbet were found. One nest contained five eggs of the owner and one egg supposedly of the scaly-throated honey-guide; the other nest contained three eggs of the barbet, three eggs attributed to this honey-guide (!) and one egg of a lesser honey-guide (*I. minor*).

If the second of these two cases is correct, it is most unusual; the three eggs identified as *I. variegatus* measure approximately 22.75 by 18 mm., while the barbet eggs are 24 by 18.5 mm. This is probably the nest referred to by Belcher (1930, p. 163) as containing 6 eggs, with one of them a honey-guide, the inference being that at the time the eggs now assumed to be *I. variegatus* were not distinguished from those of the barbet, the one honey-guide egg being the one now identified by Benson as *I. minor*.

Lybius torquatus torquatus **(Dumont).** Southern black-collared barbet.

Bucco torquatus DUMONT, *in* Dictionnaire des sciences naturelle, ed. Levrault, vol. 4, p. 56, 1817. (Brazil, error=South Africa, Goffin *in* Schlegel, Revue méthodique et critique des collections de Muséum des Pays-Bas, No. 15, Buccones, p. 4, 1863.)

The black-collared barbet is recorded as a host of the scaly-throated honey-guide in Southern Rhodesia and in the Transvaal. As already mentioned in our discussion of the eggs and egg-laying habits, Neuby-Varty (1946, pp. 345–346) saw one of these honey-guides enter a nest of a black-collared barbet, and then found it had laid an egg in it. He had examined the nest only a few minutes earlier when it had contained only a single barbet egg. Later, on December 4, he examined another nest of this barbet with four eggs of the barbet and two that he considered to be of the scaly-throated honey-guide. This attribution of the two eggs to *I. variegatus* was based on the fact that three days earlier (December 1) he had watched the barbets trying to keep a scaly-throated honey-guide away from the nest—a very uncertain basis for identification.

The late H. W. Bell-Marley collected at Isipingo, Natal, on October 29, 1930, a set of three eggs of this barbet and one egg attributed to the scaly-throated honey-guide. This set is now in the collections of the U. S. National Museum. The honey-guide egg, measuring 21.5 by 17 mm., agrees in size with the dimensions of eggs of *I. variegatus.*

Pogoniulus bilineatus nyansae (Neumann). Uganda lemon-rumped tinkerbird.
Barbatula leucolaima nyansae NEUMANN, Journ. Ornith., vol. 55, p. 347, 1907. (Bukoba, Tanganyika Territory.)

Uncertainly recorded as a host in Uganda.

Van Someren (1916, p. 234) records having found eggs of *Indicator variegatus* in nests of this barbet in Uganda, but Jackson (1938, p. 734) raises a doubt, as the barbet "bores a hole so small that neither of the two larger Honey-Guides could possibly get inside it to lay, nor could the young birds when ready to fly get out of it." Inasmuch as the eggs of *I. variegatus* are not certainly distinguishable from those of *I. minor*, the record, unsupported by further details, cannot be accepted as satisfactory.

Trachyphonus vaillantii vaillantii Ranzani. Levaillant's barbet.
Trachyphonus vaillantii RANZANI. Elementi di zoologia, vol. 3, pt. 2, p. 159, 1821. (South Africa, ex Levaillant=southeastern Cape Province, fide Vincent, Bull. British Ornith. Club, vol. 55, p. 94, 1935.)

One record, not wholly satisfactory.

A set of two eggs of this barbet with one egg of the variegated honey-guide was collected at Woodbush, Transvaal, December 3, 1920, by the late H. W. Bell-Marley. This set is now in the collections of the U. S. National Museum. The honey-guide egg measures 20 by 16 mm., as contrasted with the much larger barbet egg, 27 by 20 mm. The identification of the parasite cannot be looked upon as more than "probable."

Campethera nubica nubica (Boddaert). Nubian woodpecker.
Picus nubicus BODDAERT, Tables des planches enluminéez d'histoire naturelle, p. 41, 1783. (Nubia, based on Daubenton, Planches enluminées, pl. 667.)

The Nubian woodpecker is definitely known as a host of the scaly-throated honey-guide in central Kenya Colony.

Jackson (1938, p. 734) writes that van Someren took a nestling of the parasite from a nest of this woodpecker. In answer to my request for fuller data van Someren kindly informs me that this was in July at Ngong.

J. G. Williams (in litt.) observed a fully fledged *Indicator variegatus* being fed by a Nubian woodpecker at the Southern Uaso Nyiro River, west of Lake Magadi, Kenya Colony, in May or June 1947.

Campethera abingoni mombassica (Fischer and Reichenow). Mombasa golden-tailed woodpecker.
Picus (*Campothera*) *mombassicus* FISCHER AND REICHENOW, Journ. Ornith., vol. 32, p. 262, 1884. (Mombasa.)

One record, unfortunately without explicit locality.

Van Someren writes me that he once collected a nestling scaly-throated honey-guide from a nest of a golden-tailed woodpecker in the coastal belt of Kenya Colony in June.

Dendropicos fuscescens (Vieillot). Cardinal woodpecker.

Picus fuscescens Vieillot, Nouveau dictionnaire d'histoire naturelle, vol. 26, p. 86, 1818. (South Africa, based on Levaillant, Histoire naturelle des oiseaux d'Afrique, vol. 6, pl. 253, 1808; Grootvaders Bosch (Swellendam District, Cape Province) selected as type locality by A. Roberts, Ann. Transvaal Mus., vol. 10, pt. 2, p. 83, 1924.)

Listed as a host of *Indicator variegatus* by Gill (1945, pp. 91–92), but on what actual data I do not know. Dr. Gill informs me that he had no new data at the time of writing, and it would seem from this that his statement is not to be taken as referring to the South African, nominate subspecies of this woodpecker.

Two, more northern, races have been recorded as victims of the variegated honey-guide, as follows.

Belcher (1930, p. 167) found a nest of this woodpecker at Nyambadwe, Nyasaland, September 22, 1926, that contained two eggs of the woodpecker and one egg of a honey-guide. The latter egg measured 23 by 18.5 mm. and was thought by Belcher to be either *I. indicator* or *I. variegatus*. At the time, he was inclined to favor the former identification because of the fact that *I. indicator* was more common. Recently Benson (1952a, p. 444; 1953 p. 45) states that both he and Belcher now think that the egg is probably better referred to *I. variegatus*. The record must remain uncertain, however.

Benson (1942, p. 299) saw a variegated honey-guide following a cardinal woodpecker about from tree to tree, in close attendance, at Chinteche, Nyasaland, on September 17. "This woodpecker would in any case suggest itself as a possible host . . . and in September it is breeding."

A young fledgling scaly-throated honey-guide was seen being fed by a pair of cardinal woodpeckers in the Usambara Mountains, Tanganyika Territory, by Moreau (Sclater and Moreau, 1932, p. 665).

In Portuguese East Africa, Jack Vincent (1935, p. 12) considered that this woodpecker was the only possible host species in breeding condition early in August, at which time he collected breeding samples of the variegated honey-guide.

The Nyasaland notes refer to the subspecies *Dendropicos fuscescens camacupae* Bowen (Proc. Acad. Nat. Sci. Philadelphia, vol. 82, p. 89, 1930; Villa General Machado, Angola). The notes from Tanganyika Territory and Mozambique have to do with *Dendropicos fuscescens hartlaubii* Malherbe (Rev. et Mag. Zool., ser. 2, vol. 1, p. 532, 1849; Zanzibar).

Mesopicos goertae centralis Reichenow. Uganda gray woodpecker.

Mesopicos goertae centralis Reichenow, Ornith. Monatsb., vol. 8, p. 59, 1900. (Ndussuma, west of Lake Albert.)

Van Someren (1916, p. 234) reports having taken eggs of the scaly-throated honey-guide from nests of this woodpecker, and says that in one nest, examined in February, he found a young chick of the honey-guide. Furthermore, years later (1950) he wrote me that he collected a nestling *I. variegatus* from a nest of this host in May in Uganda. Inasmuch as the scaly-throated honey-guide is readily identified in juvenal plumage, these records can be accepted as definite evidence that the gray woodpecker is a regular host of this honey-guide in Uganda.

Mesopicos griseocephalus kilimensis Neumann. Kilimanjaro olive woodpecker.

Mesopicos griseocephalus kilimensis Neumann, Ornith. Monatsb., vol. 34, p. 80, 1926.(Kifinika, Kilimanjaro, 3,000 feet.)

One record.

Sclater and Moreau (1932, p. 665) state that a trained native collector reported (to Moreau) seeing a young *Indicator variegatus*, side by side with a fledging of this woodpecker, being fed by the latter's parents in the forest at Amani, Tanganyika Territory. The collector noted that both young birds were giving similar hunger calls.

Thamnolaea cinnamomeiventris cinnamomeiventris (LaFresnaye). Southern cliff-chat.

Turdus cinnamomeiventris LaFresnaye, Mag. Zool., vol. 6, pls. 55, 56, 1836. (Cape of Good Hope, i. e., Cape Province.)

One record, the identification of the species of honey-guide involved being not wholly certain.

Neuby-Varty informs me that he once found a nest of this cliff-chat in a partly destroyed old nest of a striped swallow. In addition to the eggs of the chat, which were in the process of hatching, there was one hard-set egg attributed to *I. variegatus*. Returning three days later he found the nest destroyed. This was near Banket, Southern Rhodesia.

Indefinite Host Records

In addition to the above host records, it may be mentioned that at Amani, Tanganyika Territory, Lack saw a scaly-throated honey-guide attempting to enter a nest hole of *Buccanodon leucotis kilimensis*, but he did not see it succeed in doing so. However, this barbet may well be found to be a victim of the parasite. Sassi and Zimmer (1941, p. 288) record a young fledged *I. variegatus* being fed by an unidentified species of woodpecker in the Songea district, Tanganyika Territory.

In the literature, the yellow-throated sparrow, *Petronia superciliaris*, is said to be a victim of this honey-guide, but the one known instance is probably really referable to the greater honey-guide, *Indicator indicator*. The data are as follows. Haagner and Ivy (1907a) collected a young chick attributed to *Indicator variegatus* from a nest of a yellow-throated sparrow in the Albany Division, Cape Province, on November 12, 1905. The bird was still practically naked, and its identification to this honey-guide rather than to *I. indicator* apparently was based on the fact that an adult scaly-throated honey-guide was seen in the tree in which the nest hole was found. The identification is not conclusive as a wandering individual of any species of honey-guide might have happened to have come to the tree. The chick was thought by Haagner to have been not more than 10 days old; it was the sole occupant of the nest. Gill (1945, pp. 91–92) lists this sparrow as a host of the variegated honey-guide, based on the above record of Haagner's.

Nestling Stage

While a number of chicks of the scaly-throated honey-guide have been found in nests of such hosts as the Nubian woodpecker (*Campethera nubica*), the golden-tailed woodpecker (*Campethera abingoni*), the cardinal woodpecker (*Dendropicos fuscescens*), and the gray woodpecker (*Mesopicos goertae*), unfortunately in most cases their discoverers made no notes on them other than in some instances stating that they were the sole occupants of the nests. It seems likely that sole nest occupancy is the rule, although there is one case known where a young olive woodpecker and a young honey-guide apparently grew up together. In this instance the birds were not found until after they had left the nest, and they were seen being fed by the adult woodpeckers. While not wholly certain, it seems that the two fledglings probably had been nest mates.

Haagner and Ivy (1907a, pp. 2–4) described a young chick, presumed to be of this honey-guide, found in a nest of a yellow-throated sparrow, *Petronia superciliaris*, in the Albany Division, Cape Province. (The identification cannot be looked upon as definite; it might have been *I. indicator.*) It was alone in the nest, was presumed to be not more than ten days old, was about 90 mm. in total length, and could hardly open its eyes, keeping them almost constantly closed. The bird was practically naked, the feathers barely beginning to sprout from their sheaths on the thighs. The tip of the bill was furnished with a pair of hard, strong, very sharp, semitransparent hooks, one on the maxilla and one on the mandible. "These tooth-like appendages measure 1.8 mm. in total length, the projecting portion of the top tooth being 0.9 mm. and that of the bottom one 0.5 mm., and are situated at the extremity of the beak; the superior aspect of the top tooth being prolonged slightly above the surface of the premaxilla, while the inferior aspect of the bottom one is slightly projected beyond the lower level of the mandible, both having the distinct appearance of being welded on to the ends. They overlap one another, thus enabling the bird to obtain a very sure hold of anything it applied its beak to . . . The hooks apparently fall off when the bird is fully adult." [20] Haagner and Ivy also noted that the nostrils have "the same swollen appearance as those of young Cuckoos, but instead of being rounded as in the Cuculidae, they are of an elongated ovate form, appearing more in the form of slits."

Nothing is known of the length of the nestling stage.

Postnest Fledgling

Very little has been learned of the postnest fledgling life of the scaly-throated honey-guide. It appears, from loose statements, that the bird either leaves the nest nearly fully grown or is attended by its foster parents until it has reached that stage. How to interpret a description without supporting detail, such as "seeing a fully fledged honey-guide being fed by" a fosterer is therefore not clear.

Moreau's native collector reported seeing a fledgling *Indicator variegatus* side by side with a young olive woodpecker, *Mesopicos griseocephalus kilimensis*, both being fed by the parents of the latter species at Amani, Tanganyika Territory (Sclater and Moreau, p. 665, 1932), and that both young birds were giving similar hunger calls.

Sassi and Zimmer (1941, p. 288) quote their collector as having observed a fledgling variegated honey-guide foraging like a woodpecker and following after its (unidentified) picine foster parent, and even attempting to climb up a tree trunk perpendicularly. This feat was barely accomplished by it, and only with much clumsy and vigorous fluttering, beating of the wings.

There is no evidence behind the statement sometimes made (as by Finn, 1919, p. 200) that the adult scaly-throated honey-guides associate with the young "when reared, and perhaps instruct them unconsciously or otherwise." Any "association," as when an immature and an adult may be found together, is no more significant than when two adults may be seen together. Finn's statement is based on one attributed to Ivy, who could not have told the age of the birds without collecting them (which he is not reported to have done). Ivy's observation is the only one known to me of several of these honey-guides being seen together.

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[20] This is probably the basis for the statement made by Mackworth-Praed and Grant (1952, p. 741) to the effect that for the first two weeks after hatching the nestling of this honey-guide has overlapping hooks on the maxilla and mandible. If they had any other data, I have not been able to learn of them.

Guiding

The guiding habit in this species is supposedly similar to that in *Indicator indicator*, but has been observed by far fewer people and is less fully described in the literature. I never witnessed any sign of guiding behavior in my own field studies of the scaly-throated honey-guide, and my experience agrees with that of numbers of other observers with far more years of field experience—such men as Chapin, Pitman, Ranger, van Someren, and Williams, to mention but a few. However, enough observations have been published to indicate that the species does guide. It would seem that it probably guides less frequently or less definitely than the greater honey-guide, but it should be remembered that the species is more difficult to find and watch and is less common than is *I. indicator*, and unless seen at close range it may be confused only too easily with the female of that species. The actual observations on record are as follows.

Near Uitenhage, Cape Province, in February 1895, Ivy (1901, p. 21) noted that "every day one of these birds [*variegatus*] came up close to our camp, and on six occasions led us to the nests of wild bees among the trees and neighboring rocks. The Honey-guide would perch on some tree and commence calling *cha-cha-cha,* to attract our attention. We followed its lead, talking to the bird all the while . . . When we got to the vicinity of the nest, the bird would not go close . . . leaving us to search for the exact spot, which was easily found by watching the passing bees."

Grant (in Sclater, 1911, p. 728) was guided to wild bees' nests by *variegatus* several times. "At the Cape the natives say that it is useless to follow a pair, as they are only calling to each other, but that it is the single birds which endeavour to attract attention. I have not been able to prove this conclusively, although it is true that all those which I followed have been solitary."

Meinertzhagen (1937, p. 745) in Kenya Colony writes of *variegatus:* "The call to attract is a *ka, ka, ka,* but we never accepted the invitation to follow."

Chapin (1939, p. 543, footnote) mentions that D. Townley informed him that he had observed guiding behavior by *I. variegatus* on a single occasion during a period of 12 years in Southern Rhodesia.

R. I. G. Attwell, Fort Jameson, Northern Rhodesia (in litt., February 19, 1951) writes that he has been led to wild bees' nests on two occasions by *variegatus.* The bird's call is said to have changed when it reached the locality of the nest.

W. L. Chiazzari (in litt., July 24, 1951) had the following experience with a male *variegatus* in nonbreeding condition (bird collected for identification) at St. Lucia Lake, Zululand, August 3, 1950:

> A track was being followed through the fairly dense bush and forest which skirts the Lake at this point when I was attracted by a somewhat agitated call from the thickets some way in front. Upon inspection I observed what was obiously a honey-guide sitting on the horizontal, protruding limb of a tree over the path. Upon approaching, the call became more and more agitated, much in the same way as most birds cry when the presence of a snake or some bird of prey has been detected. Leaving this branch it made off to another further on, following a curved line of flight. All the while, a continual stream of *chee-chee's* was kept up. Again I approached and again it moved further on repeating the same pattern of flight and call. This follow-my-leader continued in short stages for well nigh 150–200 yards from the first point of contact, then taking up a position in a larger tree it could not be persuaded to move despite the fact that I had approached to within a very short distance. It was only then that I realized that I had been following, not as I thought the lesser honey-guide, *minor*, but a species I had not encountered before—*variegatus*.
>
> Although the bush contained a number of goodly trees in the neighborhood, I was unable to locate a single hive, despite the fact that the stream of *chee's* continued unabated from the obviously excited Honeyguide.

Evidence to the effect that, like *I. indicator*, this honey-guide may also lead ratels to bees' nests comes from R. A. F. Hurt, Game Ranger, Thomson's Falls, Kenya Colony. He had previously written me that two of his reliable, trained native game scouts told him of seeing honey-guides leading ratels on four occasions; on two of these times the bird was a large one, and on the other two it was a smaller species. I pointed out that so far only *I. indicator* was known to associate in this manner with ratels, but that there was no reason for assuming that *variegatus* might not do so, and that it was even possible that some of the smaller species which do not guide humans might still enter into some such association with ratels. I suggested he borrow specimens of the various species and show them to the game scouts and see if they could tell which ones they had seen with the ratels. In a recent letter Hurt informs me that he took one of the game scouts to the Coryndon Museum, in Nairobi, where he was shown a tray containing about 40 specimens of honey-guides. The game scout immediately picked out two of them and said they were like the ones he had seen with the ratels. Both of these specimens were *I. variegatus*, and the scout further explained that he had particularly noticed the markings on the breast of the birds seen guiding the ratels.

This is the first indication that *I. variegatus* leads ratels. The case is not as conclusive as one might wish as it is not always easy, or even possible, to see the guiding bird closely enough in the field to tell *variegatus* from *indicator*, and the native's testimony might therefore be questioned, but it is suggestive and is not out of line with what might be expected.

Gill (1945, p. 92) writes that *variegatus* guides to bees' nests like *I. indicator*, but this statement is based solely on earlier statements in the literature.

Additional observations would be most desirable, as there might well be observable differences between the guiding behavior in this species and *I. indicator*, differences which might be very suggestive in arriving at a better understanding of the habit.

The details given in the discussion of the whistle-call of the present species afford material of further interest in connection with the behavior known as guiding, and should be consulted in this connection.

Food and Feeding Habits

Adult: The food of the scaly-throated honey-guide is similar to that of *Indicator indicator* and *I. minor* and consists of insects, beeswax, bee larvae, and the pollen and honey found in the bee comb. Near Kei Road, eastern Cape Province, Ranger has seen all three of these birds come to a wild bees' nest in a hollow branch of a tree and apparently feed there. He saw the present species go into the bees' nest and come out again, but could only assume that it was feeding while inside, an assumption that is rendered probable by the fact that he saw *I. indicator* enter and leave repeatedly, and was able to see that it did emerge with a piece of straw-colored comb in its bill. In the Usambara Mountains, Tanganyika Territory, Moreau (Sclater and Moreau, 1932, p. 665) saw *I. variegatus* "apparently feeding on wild figs. Actually it must have been in search of the insects they harboured, for several stomachs examined contained caterpillars, grubs, and ants, in addition to the remains of bee-combs and larvae, but no vegetable material."

Other observations may be cited. Meinertzhagen (1937, p. 745) reports that the stomach contents of specimens taken in Kenya Colony consisted of various insects, mainly Hymenoptera; there was no sign of wax or honey in the three specimens he examined. Also in Kenya Colony, Williams (in litt.) found the gizzards of his specimens to contain beeswax and insect remains, as did Swynnerton (1907, p. 290) in Gazaland, Southern Rhodesia. The latter observer trapped a male *I. variegatus* at Chirinda with a falling stone baited with a piece of guava. He supposed "that Hymenoptera of some kind must have been attracted to the guava, and that the bird, in pursuing them, settled on the twig. The stomach contained only bees-wax." In Nyasaland, Benson (1942, p. 299) found small ants in the gizzard of a scaly-throated honey-guide. Elliott and Fuggles-Couchman (1948, pp. 406, 407) list this bird as an insect feeder in Tanganyika Territory. In South Africa, Marais found only beeswax and no insect remains in the stomach contents of birds obtained by him at Knysna.

At Umtaleni, eastern Cape Province, I once saw a variegated honey-guide catching insects in midair like a flycatcher. Ranger and Skead have also made similar observations. On one occasion Ranger noted a singing (male?) bird catching insects among the nearby foliage of its call site between songs. Skead saw one come down from the call site to the edge of a stream nearby, drive away an emerald-spotted dove (*Turtur chalcospilos*), and then hop onto a partly submerged log and drink 10 or 12 sips of water. At the base of the call site, a large tree near the stream, Skead and I found numerous bits of old, dry, empty bee comb, possibly remnants of food brought to the tree by the honey-guide.

In the season of 1951 Ranger and Skead, at Umtaleni, baited a trap with a piece of comb. One late afternoon an *Indicator variegatus* was seen eagerly eying the comb in the trap and fluttering about trying to get in. It called four beats of a low whistle-call, then flew upstream. The following season one was watched entering a trap together with an *Indicator indicator*. The birds seemed not at all concerned when the lid of the trap fell shut, but began to eat the comb immediately, attempting to escape only when Ranger approached.

YOUNG: Nothing definite recorded, but the hosts undoubtedly feed the young honey-guide the same food they give their own young.

MISCELLANEOUS ACTIVITIES

Ranger once watched a scaly-throated honey-guide apparently sunning itself. It hopped up to a more exposed, less shaded, sunnier perch, turning its body and half opening one wing to catch the rays of the sun; once it altered the position of its right foot from across the twig to parallel with it, twisting as it did so.

On one occasion I saw one of these birds, that had been perching quietly on its call site, turn its tail to one side, reach down with its beak, and press on the upper base of the tail, apparently on the oil gland, and then begin to preen its wings, breast, and back plumage. A preening bird watched by Ranger used one foot to scratch its right cheek.

DESCRIPTION

ADULT MALE: Forehead, lores, cheeks, auriculars, and crown fuscous to chaetura drab, the feathers narrowly edged, but not tipped, with whitish; occiput similar but without white edgings; interscapulars, scapulars, upper back, rump, upper tail-coverts, upper wing-coverts, and remiges dull fuscous to dusky olive brown, each feather broadly edged with light yellowish olive, this color brightest and yellowest on the remiges and their greater and median upper coverts, dullest, most sooty on the interscapulars, the edgings on the back rump and upper tail-coverts broad enough to give those areas an appearance of almost solid yellowish olive;[21] two median pairs of rectrices dark fuscous to fuscous black; the more lateral ones white with dusky olive brown lateroterminal blotches on their outer webs; all but the outermost pair with some olive brown basally as well (hidden as a rule); chin and throat whitish, more or less tinged with pale yellowish, each feather with a median streak of dull dusky olive brown to chaetura drab; breast and upper abdomen similar but more strongly washed with pale olive buff, and with the dark median streaks frequently bifurcating subterminally to become edgings and tippings of the feathers enclosing a rounded subterminal whitish or pale buffy area; sides and flanks similar but with the dusky areas paler, grayer, and less distinct—light grayish olive; middle of upper abdomen and lower abdomen, vent, and under tail-coverts pale olive buff to almost whitish, especially posteriorly; thighs white; under wing-coverts whitish with some olive brown marks near the bend of the wing; iris dark brown; eyelid bluish, bill dark horn-color and becoming pinkish white basally; tarsi and toes greenish gray. Measurements in millimeters: wings 105–118, tail 67–80, culmen from base 12–13.5, tarsus 15–17.3. Weight in grams: 49, 50, 60.5.

Adult female: Similar to the male, but smaller, with the dusky markings on the chin, throat, and breast averaging paler and sparser, usually with the pale edges of the feathers of the forehead, lores, and crown less pure whitish, more washed with pale olive buff; iris grayish brown; bill olive black, paler at the base; tarsi and toes greenish gray. Measurements in millimeters: wing 98.5–109, tail 56.7–74, culmen from base 12–13.6, tarsus 14.1–15.5. Weight, 35.6 grams.

Juvenal (sexes alike): Similar to the adult female, but sometimes more yellowish, and with the rectrices and the remiges narrower, more pointed terminally, often with the throat and breast spots darker, more conspicuous than in adults.

Natal down: None.

The subspecies *virescens* resembles the nominate race in everything but size. It is considerably smaller, although the two overlap.

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[21] Zedlitz (1915, p. 8) states that frequently the upperparts are wholly without any greenish tone. I have not seen any specimens that had no greenish wash or, at least, edgings.

Measurements of males in millimeters: wing 100–105, tail 58.8–64.8, culmen from base 12.6–13, tarsus 14–15; females: wing 98, tail 56.7–62, culmen from base 12–13.6, tarsus 14–14.5.

According to Verheyen (1953, p. 117) the tail feathers are molted two pairs at a time, commencing with the median two pairs.

Native Names

Many of the natives do not distinguish this species from the better known greater and lesser honey-guides, or else authors have failed to note what names they give it. "Ndhlava" is recorded as a Zulu name for it in Natal, where the same name is also used for *I. minor.*

Greater Honey-Guide

Indicator indicator (Sparrman)[22]

Figures 1, 2,*c*, 3,*b*, 4,*a–c*, 5; Plates 1, 2, 6,b,c, 8, 9, 13–15, 22, 23, 25

Distribution

Ecological range: The greater honey-guide is primarily a bird of the dense bushveld, of tree and bush-dotted grasslands, but has also been found on occasions in less wooded savannas and in true forest. It does not penetrate far into extensive forests, however, and, accordingly, is absent from the great Congo forest, the forests of Upper Guinea, and even the much smaller evergreen forests of other parts of Africa. Thus, at Taveta, southeastern Kenya Colony, the species was fairly numerous in the thorny bushveld, but in three months spent there in 1925 I never saw it in the forested areas. It seems that it is chiefly in regions where narrow strips of forest interdigitate with bushveld or with clearings, man-made or natural (such as the forested slopes of the Karkloof Mountains in central Natal), that the greater honey-guide may range into a truly sylvan habitat.

It is absent from treeless grasslands, such as much of Basutoland, and from excessively arid areas, such as parts of the Red Sea–Somali coastal lands, the Kalahari desert, and parts of Namaqualand.

The altitudinal range of the species is from sea level to about 8,000 feet (on Mount Elgon). Sjöstedt recorded it up to 6,000 feet on Mount Kilimanjaro.

To some extent, as a contributing rather than a determining factor, the distribution and abundance of the aardvark (*Orycteropus afer*) and of the ratel (*Mellivora capensis*) affect the status of the honey-guide locally, the former apparently more so than the latter. Not only do ratels use the burrows of the aardvarks, but bee-eaters (*Melittophagus pusillus*), ant-eating chats (*Myrmecocichla*) of at least two species, and swallows often nest in the roofs of these burrows and are frequent hosts of the honey-guide.

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[22] *Cuculus indicator* Sparrman, Phil. Trans. Roy. Soc. London, vol. 67, p. 43, pl. 1, 1777. (Great Fish River, near Somerset East, Cape Province.)

Geographical range: The range of this bird encompasses most of Africa south of the Sahara, except for large evergreen forests, treeless grasslands, and excessively arid areas. It has been recorded from countless localities ranging from Senegal and Gambia and Portuguese Guinea, eastward in the thorn scrub belt north of the forest, almost to 15° N. in the French Sudan, northern Nigeria, the highlands of northwestern Cameroons, Darfur, Sennar, Ethiopia, British Somaliland, and Eritrea, and southward, skirting the great Congo forest, to the Cape Province. In Upper Guinea it has been reported from most of the countries east of Senegal (except, as yet, Liberia and Ivory Coast), but appears to be less numerous, or less generally distributed, there than in eastern, central, and southern Africa. The records from Senegal and Portuguese Guinea are without more explicit localities; in Gambia a definite specimen record comes from Nianimaru on the Gambia River; in French Guinea the bird has been found in the mountains north of Dabola; in the Gold Coast at the upper White Volta River, in Togoland at Bismarckburg; in the French Sudan, north to Fiko, east of Mopti, nearly 15° N.; in Nigeria, north to Bassa, Kafanchan, the Plateau and Bauchi Provinces; to Fort Lamy near Lake Chad; in the open tree-dotted grassy high country of northern and western Cameroons at Kumbo, Banyo, Fumban, Babadjou, and Mboula up to 5,500 feet; in Darfur, Lynes found it as an off-season visitor in the West Basin; farther east in the Anglo-Egyptian Sudan the species is known from Sennar (Roseires), Bahr-el-Ghazal (Kojali, Mongalla, Mount Baginzi), and Lado Enclave (Yei, Lado, Rejab) and Kordofan districts. Farther to the eastward, Zedlitz (1910, p. 744) writes that in northern Ethiopia and in Eritrea it occurs in the more wooded areas; it is common in the Tacazzé district in the thorny bushveld of Adiaboland and also on the eastern escarpment of the Ethiopian plateau, but has not been reported from the higher elevations of that part of Africa. It is known from many localities in most parts of Ethiopia, and even in the Juba area of Italian Somaliland.

In the Belgian Congo, Chapin has found it to occur in all the savanna areas except the Lower Congo and the open plateau of the Kivu district (where it has since been found at Ngumba by Prigogine); it is rare or absent close to the fringes of the great lowland forest, while it has been taken up to 5,000 feet in the Marungu area. It is rare in the savannas of the Kasai Province, and appears to be absent from the grasslands of the Middle Congo and Gaboon. From Kenya Colony, Uganda, Ruanda, Urundi, Tanganyika Territory, Northern Rhodesia, and from Angola southward to the Cape so many records are available, particularly from the eastern half of the continent, as to make it unnecessary to do more than state that the bird is widely distributed throughout in all suitable areas. The available records are fewer in Angola (Gambos, Chicuma, Benguella, Kutato, Mukiwa, Lwasinawa River) and still fewer in South-West Africa (Katchika, Kasane, etc.). In the Union of South Africa the greater honey-guide is widely distributed except on the high veld and the treeless western districts.

In a general sense and, in most parts of Africa, in an explicit sense, the greater honey-guide is nonmigratory. However, in Darfur, the species has been reported as somewhat seasonal. It may be that in the northern edge of its range the bird wanders northward during the nonbreeding season, from the northern savanna into the Sudanese arid belt (as defined by Moreau, 1952, p. 889), and similar local movements may occur in other portions of the continent.

Breeding Range and Season

The greater honey-guide has been found breeding in the following places and times; however, for many areas the data are very meager and the indications given for the breeding season may have to be extended.

South Africa: Many records of eggs, nestlings, and of adults collected in breeding condition show that eggs are laid from the middle of September to the second week in January, but mostly from early in October to the third week in December. Records from Cape Province, Natal, Zululand, and the Transvaal.

Southern Rhodesia: Egg records from September 24 to December 9 (near hatching?), but the season probably extends later as an adult taken on the Zambesi in December was stated by its collector to be "approaching breeding condition."

Northern Rhodesia: A female with enlarged ovary taken at Mwinilunga on March 19, and another in similar condition at Luanshya in March.

Portuguese East Africa: A female shot 50 miles southeast of Milange, Quelimane Province, on January 13 showed an ovary "coming up fast; oviduct enlarged."

Nyasaland: Chikwawa, September 28, egg; Mtongwe, December 19, fledged young; Blantyre, August 18, a year-old male "near breeding." Also an adult female "close to breeding" on September 12 and another that had "just finished laying" on April 26.

Tanganyika Territory: Apparently breeds at least from July to January. Ikoma, July 7, male with enlarged testes "coming on to breed" (other specimens, same date and locality, showed no signs of approaching reproductive activity); Igonda, October 14, male with very enlarged testes; Iringa, January 24, female collected that had "just finished laying."

Belgian Congo: Chapin (1939, pp. 552–553) found that birds collected in the Uelle district indicated that breeding extends from January to April. From near Luluabourg, in the Kasai, a young bird with wings and tail not fully grown, August 29; Elisabethville, egg record (identification of egg to this species only inferential), October 2. In the Upemba Park, males with swollen gonads have been taken in June, August, and October. In districts close to the equator *I. indicator* appears to begin breeding relatively early as compared with South African birds. Both on the north and the south sides of the Congo forest laying begins before the end of the dry season.

Kenya Colony: Suk area and central Kenya (Nairobi and adjacent areas), egg records from March 24 to May, and later, as a female was collected at Nairobi with an unshelled egg in the oviduct on July 8; nestlings reported from April through July; a fledged young bird at Lake Naivasha on November 21, and August 6; Kakamega, breeding female collected on July 10. The situation in areas like Kenya Colony and Uganda is complicated by the fact that they include regions with essentially northern hemisphere seasons, southern hemisphere seasons, and an intermediate equatorial belt where the year is divisible into four parts. Thus, the actual breeding dates when listed merely by country are apt to seem confusing. In northern Uganda one would not expect the honey-guide to be breeding in July, but from Mubendi southward it would be expected to do so from July to September or October. I am indebted to Dr. Chapin for helful comments on this complicated part of the range.

Uganda: Nestlings reported April to July; adult male in breeding condition in September; egg record at Mubendi on September 28; Aringa, West Nile District, nearly fledged nestling, April.

Anglo-Egyptian Sudan: Almost no information, but a female with enlarged ovary taken in the Mongalla area on October 18; in the Darfur area the birds were not breeding May to August, but a young bird collected in that period was assumed to have been fledged, probably in April.

Abyssinia: Breeds January to April (von Erlanger); Lake Abaya, fledgling with partly grown tail feathers, September 8.

Nigeria: Bassa, fledgling just ready to fly, April 17; Abeokuta, nestling, June 4; eggs (identity "almost certain"), February.

Songs and Calls

The greater honey-guide has a number of vocal utterances and also a mechanical nonvocal sound manifestation produced by air and feathers. The last is described fully in the account of courtship and mating and need not be repeated here.

The best known of its calls is the chattering note given when guiding. This is used by males and by females, and by fully adult and by immature birds. As far as my own observations go, and the observations of others reported to me personally or in the literature, there is no appreciable difference in the calls' pitch, intensity, or carrying power according to the sex or age of the bird. A remarkably faithful imitation of the guiding chatter may be made by shaking a partly filled pocket-matchbox back and forth lengthwise. The chatter is a repetitive series of somewhat purring, rolling, slightly rasping *churrr* notes, sometimes giving the impression, in series, of *churrra-churra* or *chwrrrt* notes. It has also been written *cutta-cutta-cutta.* Skead (1951, p. 57) notes that there is no "body movement or excitement during the calling, the bird sits quite still, often hunched up," but when first trying to attract the attention of a would-be follower the bird flits about very actively and pauses only momentarily to chatter. Some of the accounts in the literature give the impression that the bird calls while flying as well as betweeen flights, and I have experienced this myself on one occasion. At Hluhluwe Reserve, Zululand, October 16, 1950, at 9:21 a. m. a honey-guide came to me and my Zulu assistant in answer to the latter's whistling and calling. Then it began to "guide" us to a bees' nest, the total guiding tour involving seven flights from one stopping place to another. The bird was silent during the first two of these flights, but on the other five it was chattering constantly, the volume of the sound increasing each time it lit in a tree. It did not become silent until it reached the vicinity of a bees' nest, when it settled down in a large fig tree and sat quietly. However, in other cases of personal participation in guiding tours, the bird's calling was done between the component flights, even though these intervals of perching were quite brief in many instances.

The guiding call often commences quite suddenly, i. e., in cases where the bird "seeks out" the human rather than the other way about, it does not begin to call until it is quite close by. On such occasions one usually does not hear it from afar, coming closer and closer. This last situation does, however, occur at times when humans go out to attract the attention of a honey-guide. In the Hluhluwe Reserve, in Zululand, I was out in the bush with a native who was knocking sticks together, whacking on trees, whistling, and giving gutteral *aaagh-ah!* grunts, the usual procedure used in "calling" honey-guides. After some 10 or 15 minutes of this my Zulu said, "It answers now," and I could hear a far away *churrr churrr* repeated rapidly. We could not see the bird until it flew towards us, but the tree from which we first saw it come was about 150–200 feet away. At other times when out "calling" for honey-guides, the answering bird would give its chattering call but would not come to us, merely waiting for us to come to it, and on one of these occasions I estimated the distance, by counting the paces, at about 250 feet.

Some idea of the noise and the persistency of the call made by a honey-guide attempting to "interest" a native or a safari to follow it may be gathered from the numerous big-game hunters who have gone on record with comments, suggestive of exasperation, to the effect that the birds were great nuisances to them when stalking game. Apparently the large animals were often alerted by the actions of the bird, and made off without allowing the hunter to get within striking distance. There is no reason to assume that the guiding chatter of the *Indicator* conveys any specific connotation of human followers to the big game, but merely a general awareness of something strange nearby or something to be avoided.

A vocalism connected apparently with the end of a guiding tour is described by Kermit Roosevelt (in T. Roosevelt, 1910, pp. 338–339). After the natives had opened and left a bees' nest, the honey-guide which had led them to it flew straight to the still smoking opening, "uttering a long trill, utterly different from the chattering noise made while trying to attract the attention of the men and lead them to the tree." Although I have waited in the vicinity of such opened hives and have seen the birds come down to feed, I never heard any sound from them at such times.

In the present stage of our knowledge it is not safe or even possible to attempt to "read into" the data too much significance, but it may be pointed out, merely as a suggestion, that the churring call of the nestling honey-guide is not dissimilar to the guiding chatter that the bird gives later in life. This at least raises the question as to a possible common significance for the two types of vocalisms; both are connected with food-getting, the nestling call being given to the food-bearing foster parent, the guiding chatter to the "accomplice" in rendering available the food in the bees' nests. The call of the nestling is said to be kept up incessantly, almost as if it were the natural accompaniment of respiration. The guiding chatter is similarly continuous during the invervals between flights in a guiding tour— i. e., when the bird is waiting for the advent of its food-getting helper.

The variations in the intensity and frequency of this guiding chatter call are described in our discussion of the guiding behavior. Whether the following is a variant of this note is not certain, but it may be mentioned that in his account of the guiding call Skead (1951, p. 57) writes that in January and February 1948 an immature honey-guide often came to his garden. "Its call was a pretty, tripping and musical *prrreee-proo* (*oo* as in coot) made with the head brought sharply forward and downward." Later Skead decided it was only an undeveloped, more drawn-out form of the *vic-tor* note of the adult male.

The notes Skead heard from the young bird may, therefore, have been an undeveloped version of the call note (not the guiding note) of the male, a bisyllabic utterance that may be expressed as *vic-tor vic-tor*, or *whit-purr*. This note, which takes the place and fills the function of the song in oscine birds, is given only by the male bird as far as I know from personal observation or from the experience of others, and it is given chiefly (wholly in my experience) from the call posts or stud posts. That it is given elsewhere very occasionally is established, however. At Faradje, Belgian Congo, Chapin heard one give its *whit-purr* note from a tree within 100 yards of his hut, and the bird was never seen there before or afterwards. Other observers have had similar experiences, but from my own field work I would still consider it as given chiefly from the call posts. This note is usually given in series, from six to eleven notes in fairly rapid succession, with the accent on the first syllable. Each series begins with a low, much less audible rendition of the second syllable and then goes on in fuller volume with the complete notes, and ends with a subdued, seemingly partly "swallowed" first syllable. The complete song, then, may be written as *tor, vić-tor, vić-tor, vić-tor . . . vić*. At times, when a male on its call post is calling steadily—i. e., when not interrupted or frightened away by human observers or other distracting causes—these series are separated by less than a minute to a minute of silence. Thus, in exactly one hour of continuous observation a male uttered 89 *vic-tor* notes; on another occasion, 65 notes were given in 54 minutes. Once, when we were mapping locations of the secondary call posts, the bird was chased from each call post as soon as it gave a series of *vic-tor* notes there (this procedure continued for about 30 minutes). It kept up calling in spite of these interruptions and gave almost as many notes as if it had not been chased about—62 notes in 57 minutes.

When giving the *vic-tor* note the bird perched erectly, and ruffled the feathers of its throat slightly as if the initial *tor* syllable had to be forcibly expelled. Thereafter it quivered slightly, even the folded wing tips vibrating a little with each accented *vic* syllable, and the head pumped slightly back and forth with each complete *vic-tor*.

Unlike the singing of so many birds in various parts of the world, the honey-guides do not appear to indulge excessively in vocalisms early in the morning. At Umtaleni we seldom heard the *vic-tor* note before about 8 a. m., which was several hours after sunrise, although we were alert for it. The calling was kept up through the heat of the day, until about 4 p. m. when the call post was deserted until the following morning. Neither heat nor cloudiness seemed to affect the frequency or vigor of calling, but heavy rain did drive the bird into sheltered masses of vegetation where it did not continue to call. Occasionally the *vic-tor* note was heard before sunrise (5:30 a. m.) and after sunset, but these were relatively rare occurrences.

The carrying power of the *vic-tor* note was measured in a rough way by the distance from the call post at which it could be heard. In the Umtaleni Valley, Skead, Ranger, and I agreed in our independent estimates that we had been able to hear it distinctly when as much as 700 or 800 yards away from the call post, and possibly more. In the Matopos Mountains, in Southern Rhodesia, a male honey-guide calling from his post on the top of a high rocky hill was heard at least 900 yards away. These figures would suggest that a calling male could control vocally an area of several hundred acres, i. e., inform wandering females, or males, of his presence. The acreage covered varies with the distance between the widely separated secondary call posts (in the Umtaleni case the most widely separated ones were about 180–200 feet apart). Of course, not all of this acreage would necessarily be country suitable for honey-guides, but the voice of the calling male could carry across unsuitable places to more distant areas just beyond.

The *vic-tor* note is the only one that is given regularly and consistently, hour after hour, day after day for months on end by the adult male. This note has been recorded even in the nonbreeding season (late May in the Cape Province). At Umtaleni, Ranger informs me that in recent years, since he has been keeping accurate records, site-calling has not been heard in March, May, and June, and only once in April. On one occasion, at Umtaleni, Skead heard a male, which had been giving the *vic-tor* note for over an hour from its call tree, make a low but quite penetrating *shree* or *shreea* or *shreh* note, repeated a few times, and also a tripping *tr-tr-tr-tr* utterance. The *shrea* note recalls somewhat the shrill screeching of copulating birds as described in our discussion of the mating habits, but it was soft-toned and was made when the bird caught sight of another individual. It may have been more in the nature of a defensive or offensive exclamation, as it was also recorded once as given by the same individual honey-guide to a forest weaver (*Symplectes bicolor*) which flew into the call-tree and drove off the honey-guide. Although I never heard the *vic-tor* call from any but adult males, Skead and Ranger once watched two subadult (yellow-throated) birds giving this call quite far from any known call post.

As mentioned in the discussion of courtship behavior, van Someren refers to a "twittering" call by the male, and to a clicking noise made by the female with its bill.

On one occasion, when Ranger had placed a mounted specimen of a male honey-guide in the favorite call post of the male we had been watching, he noted that the bird hopped around the mounted specimen uttering a weak clucking note.

That the *vic-tor* note is subject to some geographical variation is indicated by the trisyllabic notation Myles North used to record it at Makueni, Kenya Colony. He describes the note (in litt.) as a "three-note call, repeated over and over again (often in series of seven, then with a short pause before it begins again). It sounds like *whep-tew-irr* in the rhythm of the phrase 'speak to me.' The first note is an upward-slurred whistle, and the second and third are trilled and sound much like the call of the kingfisher, *Halcyon chelicuti.*" North informs me that at Makueni the species is common, and from September onwards, at least well into November, the song of the male is one of the commonest sounds. The song is usually given from a site at the top of a big acacia, such as *Acacia spirocarpa,* but also occasionally from smaller trees or bushes.

Pease (in Ogilvie-Grant, Reid, and Pease, 1901, p. 667) once saw a greater honey-guide drumming like a woodpecker on a tree. This observation is still unique and may not have been a drumming in the woodpecker fashion but merely a matter of rapid pecking at some propolis, unobserved by the reporter, in a crevice in the tree.

Courtship and Mating

It is a singular fact, the significance of which has remained generally unappreciated, that in all the innumerable mentions of the greater honey-guide in the literature there are no published observations on this aspect of the birds' life history. Inasmuch as the courtship and mating habits of birds are so frequently revealing in the sense of explaining other parts of the annual cycle of behavior, and are so intimately bound up with the breeding habits, it was one of my chief hopes to learn something of them when I went to Africa. While I was able to learn a good deal of the mating behavior, I never saw any sign of courting. However, I am fortunate to be able to include the following data supplied me by three experienced field men.

Mr. John G. Williams, of the Coryndon Museum, Nairobi, observed a display by this honey-guide near Morogoro, Tanganyika Territory, in November 1948. In a line of trees along a road he noticed two male honey-guides courting a single female. The males seemed to take no notice of each other and did not attempt to drive each other away. As the female flew into a tree both males followed closely, settled on branches a couple of feet from her, commenced to fan and close their tails so that the white outer feathers became conspicuous, and sometimes drooped and fluttered their wings like a young bird. During this display they uttered a somewhat sharp, metallic *chip-treee* note. The female gave no evidence of interest or response, and several times flew off into another tree, only to be followed immediately by the two males. Eventually she flew away, still followed closely by the two males.

Capt. H. B. Potter, Hluhluwe Reserve, Zululand, gave me the following description of his observations of courtship activity by the greater honey-guide. The male and female birds were perching some few feet apart on a branch of a tree when the male fluffed out its feathers somewhat, raised its head feathers into a little crest, arched its wings stiffly, spread its tail, and then moved suddenly forward along the branch to the female, looking like a miniature turkey cock, but beating its stiffly arched wings rapidly as it moved. The passage of the air through the wing feathers, or the beating of the air by them, caused a low, faint *brrrr* sound. The male also gave a call similar to the guiding *churr* note, but lower and with a somewhat plaintive quality. The arched wing position used by the displaying bird makes one wonder if the yellow scapular band is thereby made more conspicuous, but on this point we have no data. When a bird has a bright color marking such as this it is usually expected that it be made use of in display.

The third note comes from Dr. van Someren who describes what he considered to be courtship behavior as follows: "Male twittering and clapping wings and chasing female; when closely approached the female would flutter wings and make a clicking noise with the bill, then dart off closely pursued by the male." As compared with the descriptions of Williams and Potter, what van Someren records appears to be more in the nature of a sexual flight than a display.

At the risk of venturing an opinion based on negative evidence, it seems that display is not commonly indulged in by this species. Otherwise, not only would others have witnessed and described it but I feel that those of us (Ranger, Skead, Pringle, and myself) who spent literally days on end watching individual males at their call posts, and even witnessing actual copulations, would have had some personal observation of it. This infrequency of display and the apparent lack of any "jealousy" or "rivalry" between the two males observed (by Williams) simultaneously displaying to the same hen suggest that courtship posturing is not a very significant or vital element of the breeding cycle in the greater honey-guide.

Indeed, my own observations, and those of my field companions in the eastern Cape Province, lead to the conclusion that the usual picture involves no display at all, but, on the contrary, reveals a most peculiar and unusual arrangement. To put it very briefly, it is this: The male chooses a conspicuous tree, usually overlooking a considerable expanse of countryside, and returns there day after day, usually being in constant residence at this post from about 8 a. m. until about 4 p. m. During these eight hours he gives his "song," a series of eight to ten *vic-tor* or *whit-purr* notes at intervals of from half a minute to a minute and a half. In my experience it is only when "singing" from such a call post that he gives these notes which are very different from the guiding chatter, and during the hours that he spends on the call post the male cannot be lured or induced to do any guiding. The females come to the call posts to be served, copulation takes place there, and then the sexes separate again. While one tree, usually the one commanding the widest view, is the chief call site, other trees within a short distance are also used as secondary posts. There is nothing at all in the nature of any companionship between the sexes; a momentary union and they part, the male going on with his *vic-tor* notes from his perch as soon as the hen has flown away. From a number of observations by Skead, Ranger, and myself in the eastern Cape Province, it is clear that not only do several hens come to the same cock bird, but also that the call post, or, as it might well be called, the stud post, is not the exclusive domain of any one individual male but is used by any male in the area, and may even be used by two at the same time without any sign of "jealousy" or "rivalry" between them.

Ranger made some observations at such a favorite call post in which he placed a mounted specimen of an adult male honey-guide. On his return to the tree the male bird proceeded to call in his usual way but after a little while became inquisitive about the mounted bird so near him. He went closer to it, hopped around it uttering a clucking sound. He did not go nearer than about six inches from it and soon seemed to lose interest and returned to his usual twig, and then flew out of the tree. In his absence an immature bird came to the call tree and showed interest in the mounted bird at once, sat beside it and pecked at it vigorously, first at the head, then the back and wings. As Ranger moved to get a better view the bird flew off and disappeared. A minute later, 11:45 a. m., the adult male returned, showed a little curiosity in the mounted bird but did not examine it closely, and for the most part disregarded it and sat quietly. At 12:21 he mounted higher and nearer to his accustomed perch. At 12:29 for the first time since 11:45 he began calling *vic-tor* and continued to do so normally until 12:53 when Ranger took down the mounted bird; from then until 1 p. m. he called from a nearby tree, when Ranger departed.

Another observation supplied me by Ranger shows conclusively that even though one male may cling to the same call post day after day, this does not prevent a second male from coming there and calling from it as well, without any sign of antagonism from either bird. The bird regularly found in this call post had a damaged bill which made it easily identifiable through field glasses. On January 18 Ranger found this individual (No. 1) and a second adult male (No. 2) perched in the same tree. No. 2 was in an inconspicuous perch under the upper branches and foliage, while No. 1 was in his usual conspicuous perch. Bird No. 2 continued to call his series of *vic-tor* notes in the usual way and No. 1 merely "looked on," as it were, looking about with the normal, curious, small movements of the head, though undoubtedly hearing and conscious of No. 2's calling. After about 10 minutes bird No. 1 flew over to its main calling tree while No. 2 remained where he was. No. 1 then began to call, followed by No. 2. Thus, there was alternate calling, but sometimes simultaneous and overlapping calling. The point of interest is that the two birds were calling from the one stud site. There was no suggestion that one answered the other; such a condition was not to be expected, and no such thing exists between males. On the contrary, in this case we have one male (No. 1), evidently established at the stud site for some time, showing no sign of any territorial "jealousy" at the presence of another calling male but merely exhibiting what may be considered nothing more than normal curiosity. The second male may or may not have established himself at this stud site, but the evidence indicates that the males of the neighborhood use the one stud post (or site). Actually, this fits in with the fact that Ranger knew of one such stud post in almost daily occupancy for at least 20 years—longer than we have any reason to think a honey-guide may live—and with the fact (described on p. 124) that Williams once found two males giving a courtship display in the same tree to the same hen simultaneously. It would be strange indeed if only one male in a sizable area were established on a call post and the others merely wandered about with no definite opportunity to attract the hens.

At the time when Ranger, Skead, and I made the observations of which the above statement is a brief summary, these were facts unrecorded in the literature. Subsequent questioning has brought out that several observers in South Africa and in Rhodesia had noticed but had not grasped the significance of the tendency of male greater honey-guides to give their *vic-tor* notes day afer day from the same spot. These scattered, incomplete observations serve to corroborate the more detailed ones of my companions and myself and make it clear that what we saw was not a peculiar, local condition but a general habit. I learned of at least one observer in Rhodesia who had seen a copulation at a call post. Because of its newness in the literature, it is necessary to record here in considerable detail at least some of the observational evidence behind the present summation.

In the Umtaleni Valley, near Kei Road, eastern Cape Province, we spent many hours daily for about 11 days at a favorite call post or stud post of *Indicator indicator*. Ranger, who knew of this post for many years, reported that it had been in practically daily occupancy for at least 20 years, both in and out of the breeding season! This is the longest continuous stud-post usage I know of, but other observers in South Africa and Southern Rhodesia have told me of similar occupancies of at least 4 to 5 years, but not necessarily in the nonbreeding season. During the 11 days of intensive observation there was always one male greater honey-guide in evidence at this post, a relatively tallish tree quite high on the side of the hilly rim of the valley, and it was always the same individual. This fully adult, black-throated bird could be identified easily because it had lost its right outermost tail feather, causing an asymetrical pattern on the underside of the tail that was readily observed through field glasses. The bird usually came to the tree and began calling about 8 a. m. and remained there until about 4 p. m.; when in the tree it usually remained in the same small section of the same branch, a very definite localization. This tree was in the lower border of an area of fairly open bush country, below which was a band of denser bush about 50 yards wide that extended down to the open grassy valley, while above the open bush country the hillside became still more open, almost fieldlike. The bird would allow the observer or observers to come within 25 feet of it, and was therefore very easy to watch. When approached more closely it would fly off to other trees nearby and would call from them for a short while, but soon would return to the favorite tree.

To take a single morning's observations: November 4, 1950; bird first heard on observer's arrival at 9:18 a. m. in favorite call post (which we may call A); in the next 54 minutes (i. e., until 10:12 a. m.) it gave 65 series of *vic-tor* notes; from 9:18 to 9:55 it sat steadily on a perch, hardly moving its position at all, then it began to move about within a radius of a few feet, but kept up its calling at intervals of not quite a minute (the calls consisted of from seven to ten *vic-tor* notes each), and also began to make a subdued but quite penetrating *shree* or *shreea* or *shrah* note, and also a tripping *tr tr tr tr;* at 10:11 it preened for the first time between calls; at 10:18 it flew off as the observer came a little too close and went to another tree (perch B) about 15 yards away, where it remained for a minute when a forest weaver (*Symplectes bicolor*) flew into the tree near it. The honey-guide gave a *shree* note and then the weaver flew at it and violently chased it out of sight; at 10:36 the honey-guide returned to the favorite post (A) returning to the identical twig it had used before; in the next hour it remained in the same tree, using six different twigs as perches and gave 89 series of *vic-tor* notes. At 11:36 the bird was deliberately approached to make it fly to see where its secondary call posts were, and it was, in effect, chased from perch to perch. It did not stop calling during this period of forced movement. Its flights pivoted from site A, the bird returning from each of the secondary posts to its favorite twig. While perched on A, the bird would allow a closer approach before flying off than at any of the secondary posts. It seemed to prefer sneezewood trees, acacias, and trees with protruding bare or dead branches.

The next morning Skead spent several hours at site A and made the following observations.

> The honey-guide was heard giving its *vic-tor* notes while I was still a good way off. Found him on the same twig at site A as yesterday. On my approach he flew 25–30 yards to perch C and stayed there while I placed some empty bee comb on a branch four feet from the ground, below and in view of his lofty perch. [His favorite perch was about 25–30 feet up.] I took up a position about 30 yards away. He was calling in the denser bush lower down on the hill in a desultory manner. I chased him from there and he flew to site A again at 9:53 where he "victored" until 10:35. He then voluntarily flew about 20 yards eastwards and recommenced "victoring." I took advantage of this change of position to remove the honeycomb, and attached it next to the favorite twig on tree A. I then went to drive him back to site A and found a female with him. Both birds seemed calm and quiet and the male "victored" as before. She showed no interest —just sat. Then she flew 10 yards or so in the direction of site A. On alighting she flicked her wings and tail up and down sharply in the way that barbets do when excited. He followed and also flicked his wings and tail on alighting but went on "victoring" about 6 feet from her. Later he flew alone to site A, saw the comb, probed it a little with his beak but did not feed, and went on calling. She followed and settled 6 inches from the comb, which she ignored but must have seen. She was lower in the tree than the male. Then he flew down to her and alighted on her back, flapping his wings, but only momentarily. They parted, she to sit a few feet from him—no sound or apparent excitement. Both then flew to a dead mimosa behind A and sat quite still about 10 feet apart while he "victored." She then flew towards me and settled in full view. He followed at once and alighted gently on her back. She was agreeable; he laid his outstretched neck and chin on her nape and head, which were also stretched forward, her tail was swung around to her right, while he fluttered his wings rapidly during copulation. Suddenly a screeching broke out, harsh and anxious in tone—*skreh-skreh-skreh*, I think from the female. Then locked thus, with him on top, they fluttered down, off balance, almost to the ground and continued thus down the slope of the hill for about 15 yards, the screeching continuous all the while. They passed from my view and silence ensued. This was at 11 a. m. and all was quiet until

> 11:10 when the male began "victoring" again in a tree below site A. The female was not seen again.
>
> I then walked up to the male and he flew off and out of sight but two minutes later was "victoring" at a subordinate site in a Kaffir plum tree. I flushed him there and soon heard him at site A, so rushed back and found him perched on top of the honeycomb I had placed there before the female came. . . . I was near enough to see his nictitating membranes working. He ate daintily, so probably was not hungry, but sometimes he pecked more lustily at the wax. . . . Then he hopped off the comb and sat on the branch alongside. . . . After 13 minutes there he hopped across to his favorite twig and sat there calmly "victoring" for the next 12 minutes when I flushed him and removed the comb.

These feeding notes, amplified and corroborated by similar ones made by Ranger and myself, show that feeding is not incompatible with call-post tenacity during the hours when it was not possible to lure the male into guiding behavior. The fact that it will not leave its call post to lead one to a bees' nest suggests, however, that the pull exerted by the call post must be fairly strong.

Two other copulations were observed at site A, one involving the same male as the first but a different female. Thus, on November 14, I made the following entry in my field notebook.

> Heard male "victoring" while I was still about 700 yards away at 8:45 a. m. He was not at the favorite site, but in another tree when I arrived; he came back to A at 9:03 a. m. and gave his series of notes at minute intervals until 10:12. At 10:13 he flew to C and then a subadult bird (subsequently found by its actions to be a female) came to him as he was calling. He flew to her and landed on top of her, but my view was obscured by the foliage; then both flew off together into the dense bush with a series of screeching cries similar to those described by Skead. Ten minutes later the male was back in tree A giving his "victor" calls.

The third observation was made by Ranger after I had left the eastern Cape Province, and extends the scope of the evidence in a most felicitous manner. The following data are taken from his letter in which he generously gave me the details for incorporation in this account.

> On November 26 I spent 3 hours at the *I. indicator* call site (A). The details are as follows. Male at site began to call "victor" when I was some 200 yards off; was not heard before though conditions were favorable. At 10:15 I came in sight of the central call-tree (A). He was in a tree 10 yards lower near the forest (dense bush) margin, uttering *vic-tor;* below him, moving about and flicking its wings constantly was another *I. indicator*, a mature female. He continued calling and she moved about on a lower level jerking her wings constantly as before; her movements were jerky . . . He then flew down on to her back and a short effort at treading was made, his wings flitting. She did not oppose this effort in any way, but it was not a success, i. e., copulation did not occur. He parted from her to perch above her and to continue calling *vic-tor*. She moved about on a lower branch, flicking her wings. She had not uttered any sound. Then, when her position was to one side and lower than his, he flew down on to her back. She received him with not the least resistance, *i. e.*, permitted his action fully. This time copulation was achieved in a most vigorous manner. His head was held

far forward past her neck as if he gripped the side of her upper neck; . . . after several seconds of treading, loud scream-chattering broke out in urgent manner and continued during the latter part of the act. It was not possible to detect which bird uttered this. Still uttering the sound they broke apart, and, one closely behind the other, they shot along in extremely rapid chasing-fleeing flight under the trees into the forest growth and out of sight; the screaming-chattering (rather in the nature of a distress utterance) came to an end. Then there occurred a drumming flight above the treetops of the forest patch; two circling movements in rustling flight were made, and this was concluded by the birds' shooting over the trees of the upper forest margin above me still "rustling," diving, in among the trees where copulation had occurred, and then disappearing in silence.

The Rustling Flight

The drumming or rustling flight is a matter of considerable interest as it or something very similar occurs not only in *Indicator indicator* but also in *I. minor* and *Melichneutes robustus*, the lyre-tailed honey-guide of the West African equatorial forests. Ranger's fortunate observation is the only one we have to date in which this performance appears to be definitely connected with the mating activities of the bird, although in the few other cases of its observation it was also given by birds at or near their favored call trees. I know of at least three such instances in South Africa and Southern Rhodesia. Van Someren's observation, cited on page 124, seems to have been a fourth instance. A similar case in Nigeria noted by Hutson (Hutson and Bannerman, 1931, p. 200) may also have been at or near a call tree, although he was not aware of the call-tree phenonemon.

Hutson writes that "once a bird was seen flying round and round a clump of tall trees making a distinct whirr with its wings, after which it perched on top of a tree to utter a series of 'sweet beers.' " "Sweet beer" is apparently the same as the notes I refer to as *vic-tor* or *whit-purr;* the tall trees may well have been call posts, and the fact that immediately after finishing the rustling flight the bird called a series of these notes further suggests the same thing. I have never experienced this note except at a call post, but I have data from other observers that indicate it is sometimes given elsewhere—possibly from "temporary" call posts or from trees which may have been call posts but were not known to be such by the observers.

Recently, Neuby-Varty made another interesting observation regarding the rustling flight. An adult male greater honey-guide was being watched giving its *vic-tor* call from a favorite tree when a second honey-guide arrived. Both birds then moved to the center of the tree where the foliage unfortunately hid them from view. After about half a minute one of them flew out at great speed and seemed almost as if it had gone mad, flying forth and back, through and around the tree, all the time making a noise in bursts of two to three seconds duration similar to that produced by a person holding a wooden slat against the spokes of a fast-revolving wheel. After about two minutes of this it flew up high and went off. The observer was unable to see just which bird made the sound, but inasmuch as he had heard the noise on other occasions he is of the opinion that it has something to do with mating, and that it is probably the female that is responsible for it. He is also of the opinion that the noise is made by the wings, not the tail.

The observations of Ranger, Neuby-Varty, myself, and a few others all suggest, but do not prove, that the rustling is made by the wings. However, the observations of Wood (1940) in Nyasaland suggest that it is the tail feathers and not the wings that are involved. Furthermore, in his case the rustling flight was more of a series of downward swoops than of fairly deep undulating dips in a circular flight. His account may be presented in his own words.

> Walking along one morning . . . I suddenly became aware of a very curious deep drum-like sound which lasted for a second or two at a time, seemingly somewhere in the air around me. *Bvooommm*—pause—*Bvooommm*, with a marked accent on the *ooo* sound decreasing on the final *mmm*. It seemed a distinct vibration of the air.
>
> Looking around, I could see nothing to account for it, and it was hard to determine exactly where it came from. I was in a somewhat open spot, a little away from the trees, and every minute or so the sound was repeated. It was fleeting and rather uncanny! I therefore stopped and stood dead still, very much awake now and on the alert. The author was soon spotted. Down from the top of the nearest big tree a Honey-Guide swooped towards me at tremendous pace, dropping to just above my head and then zooming upwards again to the same tall tree or another nearby. As it neared me and turned the tail-feathers were outspread wide apart, and the deep drumming *bvooommm* sound vibrated in the air.
>
> No other call was uttered by the bird at the time, but with my field glasses I soon identified it as it sat on the tree in the intervals of these swoops. Thinking that the observation was somewhat out of the common in the behaviour of Honey-Guides, I shot the bird for absolutely definite certainty of identification and preserved the skin, which was of a male.
>
> I may mention that this same method of attracting attention was heard by me several times subsequently in that district, but I have not remarked it elsewhere so far as I can remember. More often, of course, the birds simply uttered their usual well-known calls for attracting attention, which I may write as *Wit-purrr* and the excited chattering *Churrr* or *Tchuk-tchuk-tchuk-tchuk-tchuk*.
>
> I feel convinced that the *bvooommm* sound is produced entirely by vibrations set up by the force of the air passing through the out-spread tail-feathers, and that it is certainly not a vocal call.

Wood quite rightly compares this performance with the well known drumming of the snipe, which is definitely known to be caused by the rush of air between the narrowed outer rectrices. There is nothing peculiar in the shape of these feathers in the greater honey-guide as there is in the case of the lyre-tailed *Melichneutes*.

Another observation to the effect that the tail feathers are involved in the production of the rustling sound is the following account, contributed by Miss Clare Robinson of Cape Town in a letter to Dr. Broekhuysen, who sent it to me. "On more than one occasion a honey-guide has been known to fly low over our heads . . . rapidly opening its tail like a fan and closing it again and repeating this several times, thus making a 'wurring' noise. The bird would fly overhead and then come back over us two or three times."

Lack (1941, pp. 437–438) has brought together some data on the postcopulatory display of a number of unrelated birds (*Erithacus*, *Muscicapa*, *Columba*, and several species of Anatidae) and concludes that such display presumably has little or no survival value but is to be looked upon merely as an indication of the heightened internal condition of the birds, causing them to go through some more or less random bodily movements. Although he refers to these displays as consisting of random movements, he states that the movements given by one or both members of the pair immediately after coition are "characteristic" for the species. Have we here in the "tooting" or "rustling" diving flight of the male greater honey-guide something of this sort, comparable perhaps to the strutting and crowing of a barnyard rooster after treading a hen? Unfortunately there are no data for analysis, but there is one suggestive circumstance. As we have seen, the honey-guide usually shows little or no precopulatory display or other outward sign of internal excitement, and if we may assume that coition is ordinarily and regularly accompanied by some such heightened tension, may it not find expression afterwards? It is not possible at present to do more than raise the question; a definite opinion would be quite premature.

It seems, from the data presented in detail above, that we may include the greater honey-guide (and, apparently also the lesser and the scaly-throated species, although here the evidence is much less ample) among those birds that show no true pair-formation, the sexes meeting merely for copulation and then parting. Lack (1940b, pp. 269–270) has divided these birds into four types: those in which the sexes meet at communal display grounds or "leks" (examples of which are known chiefly among the gallinaceous birds, some limicoline species, a few hummingbirds, and a few passerine species of unrelated families); those in which the male is isolated and displays conspicuously and the female comes to him (as in some gallinaceous birds, birds-of-paradise and bower-birds); those in which the individual hens visit the flocks of males but the individual males have no established stations (as in the boat-tailed grackle); and parasitic birds (like the cowbird and the European cuckoo) in which at times, but not regularly, there may be formed a more lasting bond between the sexes.

It appears that the situation in the honey-guides partakes to some degree of the characteristics of several of these groups, and agrees entirely with none. More information, especially on all the species other than *Indicator indicator*, may well reduce the apparent uniqueness of our present picture, but for the time being we can only think of it in light of what we now know. Thus, we have seen that in some cases the male honey-guide is isolated and is remarkably constant in his attendance at a particular call post, and, while he does not display conspicuously (usually not at all), he does give his *vic-tor* notes continuously from there. He acts ostensibly as if the site were his own individual post in every way except the very important one that he shows no sign of jealousy or exclusiveness regarding it and makes no attempt to drive off a second, nomadic (?) male that may at times use it simultaneously with him.

Seasonal Movements and Site Tenacity

There is no evidence that the greater honey-guide is migratory, and, in fact, in many parts of its range it is recorded as present throughout the year. In some areas, however, there is some evidence suggestive of local seasonal movement. Thus, in the Abyssinian lowlands and in the adjacent Bogos district von Heuglin (1869, pp. 767–769) thought it disappeared during the dry season—December to the middle of April. In the Darfur area in the Anglo-Egyptian Sudan, Lynes (1925, p. 351) considered the species as an "off-season visitor" only. In Northern Rhodesia, White (1946, p. 72) suggested that the observed variation in local abundance or scarcity might be due to periodic failures of the flowering of *Brachystegia* and *Isoberlinia*, which would affect the number of bees and thereby the welfare of the honey-guides. In Southern Rhodesia, Priest (in litt.) found the birds to be "local migrants" and "only a few remaining, as there are far fewer about in winter."

Just what or how much effect the abundance of bees has on the numerical status of the greater honey-guide is difficult to say, as there are usually other factors operating simultaneously which cloud or may even change what correlation might otherwise exist. In the Hluhluwe Reserve, Zululand, Capt. H. B. Potter informed me that there were many more wild bees' nests and many more honey-guides before about 500 natives had been sent in to combat nagana, the sleeping sickness of cattle. An unplanned result of this was that these natives greatly depleted the available supply of wild honey by persistently robbing all the wild nests they could find with the aid of the *Indicators*. After this, the honey-guide population declined very noticeably. Captain Potter's statement is a considered opinion but is not based on actually recorded data. On the other hand, in Northern Rhodesia, White and Winterbottom (1949, p. 64) found crude but fairly well marked negative correlation—the honey-guides being less numerous in areas of high wax production, like Mankoya and Balovale, than elsewhere, as in the Rufunsa-Lunsemfwa areas.

My personal experience indicates that a fair percentage of the honey-guides may be somewhat nomadic (especially the subadult birds), only fully adult males being found established on call posts. The fact that at these call posts the same individual bird may be found day after day with great regularity for long periods of time might suggest territorial behavior, but this is certainly negatived by the complete lack of jealousy or exclusiveness with regard to other males at these sites, and by the fact that while one individual may be the only one definitely "established" there, other males may use it simultaneously even though only temporarily.

In the Umtaleni Valley, near Kei Road, eastern Cape Province, Gordon Ranger banded an adult male honey-guide that was present day after day on a definite call post to which it adhered throughout each day. Later, during the nonbreeding season, the same individual was encountered about 1½ miles away, where it led him to a wild bees' nest. Another marked individual, a female, was retaken over a period of months at places as much as 3 miles apart in the Umtaleni Valley. These observations give us the only reliable indication of the area covered by a single bird, and even here there is no proof that the bird might not have ranged still farther afield.

Evidence to the effect that an adult male giving the typical *vic-tor* call may be nomadic comes to me from Skead, who saw and heard such an individual during its passage through King William's Town. The bird was there for only one day, but during that day acted much like an individual established on a call post.

That the same individual may visit the same bees' nest at short and also at fairly long intervals, and that several individuals may repair to the same hive, is shown by some of Ranger's recent work involving banded birds. Thus, individual A94 was trapped at a bees' nest on June 12 and retaken there two days later; bird A96 was trapped at the same hive on June 17 and again on July 26; individual A99 was taken at the same bees' nest on September 26 and again on October 9. The trap at this particular bees' nest remained in operation day and night from June 12 on, and was visited daily. In spite of these daily inspections, honey-guides were seen there relatively infrequently. Other honey-guides marked and released were taken again in the same place 79 and 116 days later, indicating a tendency to remain in the same general area over considerable periods of time.

Eggs and Egg Laying

The eggs of the greater honey-guide are pure white, quite glossy, oval in shape (i. e., there is relatively little difference between the "small" and the "large" poles), and vary in size from 22.7–26 by 16.8–19.6 mm., the largest one 26 by 19.6 mm., the smallest one 22.8 by 16.8 mm. The eggs of this species are not always certainly distinguishable from those of *Indicator variegatus* and *I. minor*, and differ from them only in being usually larger. It would be difficult if not impossible to separate with any certainty a small egg of *I. indicator* from a large one of *I. minor* or *I. variegatus*, as the maximal measurements of *I. minor* eggs are almost as large (22.5 by 17.9 mm.) as the minimal ones for *I. indicator*.

As far as I know no one has ever taken a fully shelled egg from the oviduct of a shot female, so, in a sense, there are no absolutely authentic eggs of the greater honey-guide in any collection. The eggs are definitely known, however, from descriptions of examples that were allowed to hatch and were subsequently identified by the chicks when they acquired their juvenile plumage. The impossibility of identifying the egg, as such, in museum collections enters all too often into our discussion of the various host records given below. In many cases, however, the eggs were collected by experienced field workers who knew the local fauna well and were satisfied that *Indicator variegatus* did not occur in the localities involved. To reject their identifications of the eggs as *I. indicator* in all cases would call for needlessly rigid standards. It remains true, nevertheless, that in many of these cases the identification is arrived at by elimination rather than by more positive and direct methods. It would be well, to settle all doubts and to satisfy all scruples, if someone were to collect an oviduct egg as a positive reference specimen.

Inasmuch as the eggs of honey-guides and those of their nearest relatives—the barbets, woodpeckers, etc.—are always pure white, and inasmuch as the bulk of their victims belong to the white-egg-laying piciform and coraciiform families, it is not possible to look upon this as a case of adaptive egg similarity between parasite and victim. While most of the victims are birds that lay white eggs, there are others that do not. Among the latter group may be mentioned *Phoeniculus purpureus*, *Rhinopomastus cyanomelas*, *Hirundo albigularis*, *Monticola rupestris*, *Cinnyricinclus leucogaster*, and *Spreo bicolor*. The last named is certainly a frequently victimized species. It may be argued that as most of these birds nest in the darkness of long tunnels, or at least in the dense shade of ledges, color adaptation in eggs may not have been of selective value in the history of the honey-guides. The eggs of the hosts are larger in some cases, smaller in others, than those of the parasite.

The number of eggs laid in one season by one female is unknown, but that the number may be fairly large is suggested by an adult female (collected by J. G. Williams at Nairobi, Kenya Colony, on July 8, 1948) that had an unshelled egg in the oviduct, three discharged egg follicles in the ovary, and four ovarian eggs more or less enlarged and yolking. Nothing is known as to the interval between eggs, although uncritical, gross examination of two discharged follicles in the ovary of a hen I shot in the Kakamega district of Kenya Colony showed so little difference that it seemed unlikely that there could have been more than a day or two between them.

Whether or not all the eggs of a single female honey-guide are deposited in nests of a single species of victim is not known. That the egg is laid directly into the nest of the host seems a valid assumption. Two observers have told me of seeing a honey-guide entering the nest hole of its victim and then subsequently have examined the nest and found the parasite's egg in it. No one has reported seeing a honey-guide fly into a nest with an egg in its bill. Even in the case of the European cuckoo, where so many writers have repeated the old story of the bird laying its egg on the ground and then putting it into the nest with its bill, the evidence is all for direct laying in the nest. The only reason I stress this point is that the early and quite unreliable notes of the Verreaux brothers, quoted by Hartlaub, Des Murs, and a few other authors, include a statement to the effect that the hen lays its egg on the bare ground and then carries it in its bill to a previously located fosterer's nest, from which it then removes an egg. The Verreaux brothers also state, without any supporting evidence, that one female honey-guide laid three eggs, each one in the nest of a different species of victim. Inasmuch as a century later we have no information as to the details of oviposition and host specificity, these unsupported statements cannot be accepted as factual.

An incomplete observation, related to me by Mr. H. M. Millar of Durban, suggests the possibility that the male honey-guide may at times accompany the female when the latter is about to lay. As described in the discussion of the black-collared barbet, *Lybius torquatus*, as a host of this bird, Millar once saw a "pair" of these honey-guides at a nest hole of the barbet. The latter chased away the male honey-guide whereupon the female *Indicator* slipped into the nest. Unfortunately, it was not possible for Millar to examine the contents of the nest subsequently. Purely from other aspects of its life history, I find it difficult to believe that the male regularly accompanies the hen to nest holes of potential victims, as there are no data suggesting anything comparable to mating in these parasites. That the male should act as a foil, to draw off the barbets on guard while the female deposits her egg, seems like too good a story not to have entered into the recording of whatever may have actually transpired.

Usually only one egg is laid in any one nest (46 cases). The only instances I know of where more than one greater honey-guide egg has been found are the following two, further mentioned in the accounts of the host species. In Southern Rhodesia, Neuby-Varty found a nest of an African hoopoe with three eggs of its own and two of the greater honey-guide. The honey-guide eggs were almost identical in size (24.5 by 19.25 mm. and 24.5 by 19.5 mm.) and may have been laid by one bird. At Bloemhof, in the Transvaal, Plowes found three honey-guide eggs in a nest of a scimitar-bill, *Rhinopomastus cyanomelas.* In this case, judging by the variations in their dimensions, it seemed that they were laid by three different individuals.

There are statements in the literature that suggest that when laying into a nest the honey-guide removes an egg of the victim's, but these are not based on any real observations and are merely inferences made subsequently to explain the small number of the host's eggs in the nest. Thus, to take but one example: Near Essexvale, eastern Cape Province, the usual clutch of the pied starling, *Spreo bicolor,* is five eggs; yet, during three successive years, in every starling nest that had a honey-guide egg, Brian Stuckenberg of Rhodes University College found either three or four eggs of the starling. He attributed this fact to the possibility of the honey-guide having removed an egg or two of the host's when laying its own. He looked carefully for bits of egg remains on the ground outside the nest holes but never saw any, and concluded that if the parasites did remove any eggs they took them off some distance before disposing of them. On the other hand, we have the fact that in many of the parasitized clutches the number of eggs of the host is not less than in nonparasitized nests of the same species. In the related *Indicator variegatus* we have some direct, positive evidence that no egg of the host is removed by the laying parasite. That the greater honey-guide may steal an egg from a nest is suggested by one somewhat tangential observation. Skead (1951, p. 61) has recorded seeing a male *Indicator indicator* fly from a nest of a bar-throated warbler (*Apalis thoracia*) with an egg in its bill. This case, unique in recorded data, is a little different from the matter of removal of a host's egg to make room for one of the parasite's, as it was a male bird that stole the egg and it involved a species not known to be parasitized by the honey-guide.

There is a good deal of evidence that the honey-guide punctures, either with its bill or its claws, the eggs in a nest when laying one of its own. Data on 20 such cases are included in the discussion of each of the various host species involved—*Halcyon chelicuti, Melittophagus* *pusillus, Melittophagus bullockoides, Phoeniculus purpureus, Rhinopomastus cyanomelas, Upupa africana, Campethera abingoni,* and *Myrmecocichla aethiops.* That this practice is not invariably followed is attested by the fact that in a still larger number of cases no such egg damage was observed. The damage, when damage is done, looks more like bill peck marks than claw marks as the latter would tend to produce longer and more irregular cracks and breaks than are described in these cases. There still is much to be learned of this matter as the variation in the experience of individual collectors is too great to be "explained away." Thus, in Southern Rhodesia, Neuby-Varty considers egg pecking to be so much the regular procedure that the young honey-guide, on hatching, seldom has to contend with any nest mates. Years ago Haagner and Ivy (1907b, p. 103) concluded that "all the Honey-Guides break the eggs of the foster parent to make room for their own, wherever possible." Yet other collectors, also with considerable experience, have not noticed any such tendency. That the pecking, when it occurs, is done by the adult and not by the chick when newly hatched is proved by the fact that it exists prior to the hatching of the honey-guide egg. To present the situation in a more telling manner, it may be said that no case of egg pecking or clawing is known for the lesser honey-guide (*I. minor*) in an equal number of parasitized nests. It is conceivable that eggs of certain species of hosts are more regularly pecked than others; the number of instances are too small in these cases to be of statistical significance but they may be worth mentioning; thus, pecking of the hosts' eggs occurred in four out of six parasitized nests of the hoopoe, *Upupa africana,* and in only one out of eight nests of the pied starling, *Spreo bicolor* (only nests with eggs were counted). If it should develop that there is a real difference in the treatment different host species receive, it would suggest two possibilities—that eggs of some species are harder to puncture than others or that some individual honey-guides are more prone to peck holes in the eggs than others and that they have some degree of individual host specificity.

In some of these instances of egg pecking the damage might almost be dismissed as accidental due to the supposedly hurried actions and movements of the honey-guide, while in others it is clearly not a casual, perfunctory matter but bears every mark of being a determined effort to destroy the potential viability of the host's eggs. Thus, in one nest of an African hoopoe, *Upupa africana,* one of the two hoopoe's eggs had no less than 12 peckings and the other had 4. Most of the pecks had not gone through the inner membrane, but in one of the eggs two peck holes, larger than the others, had penetrated the membrane.

In spite of the paucity of data on egg laying, there are some cases on record that indicate that the laying by the host and by the parasite are not always well synchronized. Thus, in one nest of *Upupa africana*, Neuby-Varty records the honey-guide egg was fresh and the three eggs of the hoopoe were well advanced in incubation, showing that the parasite must have laid in the nest a considerable time after the victim had commenced to incubate. On the other hand, we may point to the case of a nest of *Melittophagus pusillus meridionalis* containing three fresh eggs of the host together with a recently hatched honey-guide chick. Another similar case was found at Discovery, Transvaal, by G. H. Patten.

There is a notable lack of recorded observations on the approach of greater honey-guides to the nests of their victims compared with the numbers of such cases described for the lesser honey-guide. This may mean that *I. indicator* actually has far fewer fights with its victims or that it lays its eggs very early in the morning and has therefore gone unobserved in the act by naturalists. It is evidently not mobbed by other birds the way *I. minor* frequently is.

Nothing is known as to the length of the incubation period. Farther on (p. 192) we give some evidence suggesting that in the related *I. minor* the period is from 11 to 16 days. This is a point in the life history of all the honey-guides about which data are badly needed.

Hosts or Victims

The known victims of the greater honey-guide's parasitism number 30 species, or, including subspecies, 35 forms. The hosts are mostly hole-nesting birds—two species of kingfishers, four of bee-eaters, two of wood hoopoes, one of hoopoes, five of barbets, four of woodpeckers, two of thrushes, four of starlings, and two of weaver finches. Of the remaining species, two of the three swallows are almost hole-nesters in effect as their nests are closed, and hence, dark inside, while the third swallow and one thrush build in shaded crevices under rocks and ledges. Only one of the recorded hosts, a drongo, builds an open nest in an open position, and this one record seems to be erroneous. The number of host species undoubtedly will be increased as more field data are recorded. From many parts of Africa there are available no host records whatever—areas as rich in bird life and as large as the Belgian Congo, Tanganyika Territory, the Anglo-Egyptian Sudan, Abyssinia, and all of West Africa, except for a very few records from Nigeria. It follows that it is premature to say which species are the most frequently parasitized, but of those now known to be victims of the greater honey-guide the following are the ones with the largest number of records (out of a total of 96 instances): *Melitto-*

phagus pusillus 19; *Spreo bicolor* 12; *Upupa africana* 9; *Melittophagus bullockoides* 6; *Petronia superciliaris* 5; *Phoeniculus purpureus* and *Campethera abingoni* 4 each; *Lybius torquatus* 3; *Campethera nubica* 2+; *Hirundo cucullata* 3+; *Halcyon albiventris*, *Tricholaema leucomelan*, *Dicrocercus hirundinus*, *Trachyphonus vaillantii*, *Campethera taeniolaema*, *Myrmecocichla aethiops*, and *Myrmecocichla formicivora* 2 each. Of the other hosts only single records are known to me.

While it appears that the bee-eaters, hoopoes, wood hoopoes, barbets, woodpeckers, and starlings are of great importance in the economy of the honey-guide, we cannot say how much of a check on their natural increase the parasitism of the latter may be. At times, and locally, the greater honey-guide may be a serious factor in the population status of some of its common victims, as is pointed out in the discussion of *Melittophagus pusillus* and *Hirundo cucullata*, but even in the best known cases the data are too few to permit of any generalizations at present.

Halcyon albiventris albiventris (Scopoli). Brown-hooded kingfisher.

Alcedo albiventris Scopoli, Deliciae florae et faunae insubricae . . ., pt. 2, p. 90, 1786. (New Guinea, error=Natal, see Schlegel, Muséum d'Histoire Naturelle des Pays-Bas, Revue Méthodique . . ., No. 17, Alcedines, p. 31, 1863.)

In a letter to C. J. Skead, Brian Stuckenberg reports that on two occasions, once in 1937 and once in 1947, near Essexvale, eastern Cape Province, this kingfisher was found to be parasitized by the greater honey-guide. In each case the eggs were found and collected.

Halcyon chelicuti chelicuti (Stanley). Striped kingfisher.

Alaudo chelicuti Stanley, *in* Salt, A voyage to Abyssinia, Appendix, p. lvi, 1814. (Chelicut, Abyssinia.)

Near Marandellas, Southern Rhodesia, early in October 1949, Neuby-Varty found a nest of this kingfisher containing one fully feathered young greater honey-guide and three pecked eggs of the host. This is the only instance known to me of this bird as a victim of the honey-guide.

Aerops boehmi (Reichenow). Boehm's bee-eater.

Merops (*Melittophagus*) *boehmi* Reichenow, Ornith. Centralbl., vol. 7, p. 62, 1882. (Bumi, Tanganyika Territory.)

Recorded, not with absolute certainty, as a host of the greater honey-guide in Nyasaland by Benson (1950), who writes that at Chikwawa on September 28, 1944, he collected two clutches of eggs of Boehm's bee-eater, one of which had, in addition to two fresh eggs of the *Aerops*, a third, dissimilar egg, also fresh, measuring 23.1 by 18.0 mm. (as compared with 18.2–19.2 by 15.2–16.1 mm. for the bee-eater's eggs). This egg is rougher in texture, more oval, and somewhat glossier. Benson and Pitman, to whom he gave the eggs, agree "that there is no reason to think that it is not attributable to a honey-guide. The measurements agree with those of the Black-throated Honey-guide, *I. indicator*. It is unlikely that in this particular locality, which I know well, the Scaly-throated Honey-guide, *I. variegatus,* whose eggs would appear to be of similar size [see Roberts, 1939, pp. 101–102] could have been the parasite concerned."

More recently Benson (1953, p. 45) lists this bee-eater as a host of *I. indicator* without expressing any doubt about it.

Melittophagus pusillus meridionalis Sharpe. Southern little bee-eater.

Melittophagus meridionalis SHARPE, Catalogue of the birds of the British Museum, vol. 17, p. 45, pl. 1, fig. 4, 1892. (Pinetown, Natal.)

This bird is a frequent host, and perhaps is the species most often victimized in southern Africa. I have data on no less than 19 such parasitized nests.

Near Durban North, Natal, Walter J. Lawson (in litt. to C. J. Skead) found several such cases; in four of them the bee-eaters' eggs were punctured, apparently by the honey-guide when laying.

Plowes (in litt.) informs me that at the Matopos Research Station, about 20 miles from Bulawayo, Southern Rhodesia, he opened four nests of the little bee-eater and found all of them to be parasitized by the greater honey-guide. One nest, examined on November 13, contained only a young chick of the parasite; one found November 26 had one honey-guide egg with three of the bee-eater; while two nests opened on December 9 contained a lone chick of the honey-guide in one case and one honey-guide's egg with four of the bee-eater's in the other one. The fact that no great search was made for bee-eater's nests yet such a large percentage was found victimized suggests that this species must be a frequent victim of the greater honey-guide in Southern Rhodesia.

This bee-eater has also been found to be parasitized at the Wankie Game Reserve, Southern Rhodesia.

A. W. Vincent (1946, pp. 323–324) has taken eggs, presumably of *I. indicator,* from nests of this and two other species of bee-eaters.

A. Roberts (1939, pp. 100–102) found a young chick of the greater honey-guide in a nest of this bee-eater together with three fresh eggs of the bee-eater at Pretoria on November 4, 1910. It was this record that Haagner erroneously published as from a nest of the Cape sparrow, *Passer melanurus.*

Benson (1950, pp. 478–479) notes that his native collector obtained at Mitongwe, Ncheu district, Nyasaland, on December 19, 1949, a fledged young greater honey-guide which was following and soliciting food from a little bee-eater. He further relates that at Mpinganjila's village, near the north end of Lake Pamalombe, A. H. Paget-Wilkes "found a fully fledged honey-guide at the end of a nesting hole two feet long excavated in the side of a pit belonging to a little Bee-eater *Melittophagus pusillus*. The nestling was dark green on the back, with sulphur-yellow throat, underparts otherwise white." This obviously was *I. indicator*.

At Discovery, Transvaal, Graham Patten (1952) found a nest of this bee-eater on November 11, 1951, containing a young, still unfeathered chick of *I. indicator* two or three days old and four eggs of the host. This chick, kindly sent me by its finder, is the basis for our figure 4,*a–c*.

Another case, in which the specific identity of the parasite is only surmised, but probably correctly, is the following. At Umhlanga Rocks, Natal, I. C. Tait (1952) dug open a nest burrow of a litttle bee-eater on December 9, 1951, and found the occupant to have been brooding five eggs—four of its own— each of which contained a dead and dried-up half-developed embryo. The larger egg agrees in dimensions with those of *I. indicator*. The four *Melittophagus* eggs all had dents or cracks in their shells.

Melittophagus bullockoides (Smith). White-fronted bee-eater.

Merops bullockoides A. Smith, South African Quart. Journ., ser. 2, p. 320, 1834. (South Africa.)

A. W. Vincent (1946, pp. 307–308) found two nests of this bee-eater in the Umvuma district, Southern Rhodesia, on September 24. Each nest contained five eggs of the owner and one of a large honey-guide, probably *I. indicator*. The two parasitic eggs were fertile. Two of the bee-eater's eggs in one nest and three in the other were addled, having tiny punctures as if pecked or clawed. The two *Indicator* eggs measured 24.0 by 18.5 and 25.0 by 18.4 mm. On September 21 of the following year a third nest was found with four eggs of the owner and one of the honey-guide, the latter being relatively broader than the two of the previous year, measuring 23.8 by 19.4 mm. The eggs of the bee-eater averaged 22.6 by 18.5 mm.

B. M. Neuby-Varty has also found the white-fronted bee-eater to be parasitized by the greater honey-guide in Southern Rhodesia. He found two parasitized nests in the same "colony" in a high bank on the Winimbe River, Marandellas, in early October 1946, each containing three eggs of the bee-eater and one of the honey-guide; all were fresh.

At Lake Naivasha, Kenya Colony, on August 6, 1950, John G. Williams found a fully fledged *Indicator indicator* being fed by a pair of white-fronted bee-eaters.

Dicrocercus hirundineus hirundineus (Lichtenstein). Swallow-tailed bee-eater.

Merops hirundineus Lichtenstein, Catalogus rerum naturalium rarissimarum . . . , p. 21, 1793. (No locality; Orange River (ex Levaillant; see Peters, 1945, p. 229).)

Two records, one not absolutely certain as to the identification of the parasite.

A. W. Vincent (1946, pp. 307–308) found a nest near Elisabethville, Belgian Congo, on October 2 containing three eggs of the bee-eater and one that probably was a greater honey-guide's. The parasitic egg was more elongated, less rounded, than those of the host, 24.1 by 18.3 mm. as compared with 20.4 by 18 mm. At Dedza, Nyasaland, in December 1951, Benson found a nest of this bee-eater containing one young greater honey-guide almost ready to fly and five punctured eggs of the host.

Upupa africana Bechstein. African hoopoe.

Upupa africana Bechstein, Kurze Uebersicht . . . , vol. 4, p. 172, 1811. (Congo to the Cape.)

Recorded as a host of the greater honey-guide in South Africa, Southern Rhodesia, and Kenya Colony. The actual cases known to me are as follows.

The Attwoods (1945, p. 209) found a fledged chick of this honey-guide being cared for and fed by hoopoes in a garden at Johannesburg. Mr. K. F. Gibbs, of Hill Crest, Natal, in a personal communication, mentions knowing of an instance of the African hoopoe being victimized by a greater honey-guide. Whether this is the same case as the above or is still another record I cannot say.

Gilges (1939) found in a termite mound near Johannesburg a nest of the hoopoe containing a completely unfeathered young honey-guide, the shrivelled remains of a dead nestling, and three eggs of the hoopoe. The honey-guide, being as yet unfeathered, could not positively be identified as to species and is listed merely as a "honey-guide"; it had sharp curved hooks on both the maxilla and the mandible. It must be looked upon as included here on uncertain grounds, chiefly because *I. indicator* is the only species of honey-guide known to parasitize the African hoopoe.

In the Oologists' Record (September 1949, p. 45) is an anonymous note telling of the receipt of a set of two eggs of the African hoopoe with one of the greater honey-guide, unfortunately with no indication of date or locality. The eggs were laid in a natural hole in the ground and the host's eggs had holes pecked in them.

In Southern Rhodesia, Neuby-Varty tells me he has yet to find a nest of this bird that is not parasitized by the greater honey-guide. Data on four nests, all from the Marandellas area, kindly supplied by him, are as follows.

Set 1: Early October 1948, nest in hole in the side of a termite mound contained one egg of the parasite and four of the host, all of the latter pecked.

Set 2: Early October 1948, nest, a hole in the ground, contained two fresh honey-guide eggs and three of the host, the latter all pecked.

Set 3: September 29, 1946, nest, a hole in the ground, contained one fresh egg of the parasite and three hard set eggs of the host. In this case the honey-guide not only did not peck the hoopoe's eggs but also must have laid in the nest considerably after the host had begun to incubate.

Set 4: Early October 1949, nest, a shallow hole in the side of a bank, contained one young partly feathered honey-guide and four pecked eggs of the hoopoe.

At Lake Naivasha, Kenya Colony, November 21, 1951, in the middle of the short rainy season, Belcher was asked to identify a young bird in a hoopoe's nest. He writes me that the nest was in a deep hollow, about 10 feet up in a tree, and when the young bird was taken out it proved to be a fully feathered young *I. indicator*. The hoopoes were feeding it regularly. This was the only time Sir Charles had found the greater honey-guide breeding at any time of the year other than during the long rains.

Phoeniculus purpureus (Miller). Red-billed hoopoe.

Promerops purpureus Miller, Icones animalium . . . , pl. 9, fig. 52, 1794. ("India orientale," error; probably based on a Levaillant bird from Knysna.)

Three races of the red-billed hoopoe have been reported as victims of the greater honey-guide.

Haagner and Ivy (1907b, p. 103) record an egg of "*Indicator sparrmani*" found in a nest of this wood hoopoe, apparently in the Albany Division, Cape Province, and unfortunately without other data. This record refers to the nominate subspecies of the host.

A. Roberts (1939, pp. 100–102) records a set of four eggs of the Angolan race of this hoopoe, *Phoeniculus purpureus angolensis* (Reichenow),[23] with one of the greater honey-guide, collected at Pietersburg, Transvaal, December 15, 1933, now in the collection of the Transvaal Museum. The identification of the honey-guide is not wholly certain, however, as Roberts states at the end of his list of host records that some of the honey-guides' eggs may be *I. variegatus*. The same set is referred to by Priest (1948, pp. 63–64).

Neuby-Varty sends me the following data. At Umvukwe Ranch, Banket, Southern Rhodesia, in October 1945, he examined a nest of the red-billed hoopoe in a natural hollow in a tree. It contained one egg of the greater honey-guide, hard set, and five eggs of the builder, all of them with holes pecked in them.

Serle (1950 a, p. 88) records eggs "almost certainly" of *I. indicator*, one in each of two nests of the red-billed hoopoe at Abeokuta, southwestern Nigeria, in February. One nest contained two blue eggs of the host; the other had three, in addition to the white one of the honey-guide. This record refers to the Nigerian race, *Phoeniculus purpureus guineensis* (Reichenow).[24]

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[23] *Irrisor erythrorhynchus* var. *angolensis* Reichenow, Die Vögel Afrikas, vol. 2, p. 339, 1902. (Kakonda.)

Rhinopomastus cyanomelas cyanomelas (Vieillot). South African scimitar-bill.
Falcinellus cyanomelas Vieillot, Nouveau dictionnaire d'histoire naturelle, vol. 28, p. 165, 1819. (Namaqualand.)

One record is known to me, one that fortunately is very fully implemented with observational data. Plowes (1948) is the discoverer and recorder of this case, and his account is so full of interest that it is given here in its original wording.

> On 24 November, 1946, while on the banks of the Vaal River at Bloemhof, Transvaal, I saw a Scimitar-bill Hoopoe (*Rhinopomastus c. cyanomelas*) fly from an old Barbet nest. This was situated 5 feet from the ground in a species of Rhus which grows in the thick bush lining the river. The nest hole was about 9″ deep, and on the padding of hair and fur at the bottom were the following: one whole, but cracked, Scimitar-bill egg; the thin end of a second Scimitar-bill egg; two whole, but cracked white eggs; the two halves of a third white egg which had just hatched; and a Honeyguide chick about one day old.
>
> The Scimitar-bill eggs are . . . blue . . . , are glossy, and have pores spaced about 1 mm. apart. The half egg had been broken whilst still fresh and the whole egg had had its development arrested due to the cracking of the shell. The broken egg measured about 16 mm. in width whilst the whole one was 22.0 by 15.3 mm.
>
> The broken halves of the Honeyguide egg fitted together almost perfectly, and it now measures 21.7 by 17.4 mm. The other two eggs measure 24.0 by 17.6 and 24.3 by 18.8 mm. respectively. These two eggs had failed to develop, so that the cracking presumably took place soon after they were laid. All three eggs were discoloured by soiling in the nest, although originally white, with practically no gloss, and with small deep pores irregularly spaced about 1–2 mm. apart. They were more or less equally rounded at either end. It would appear from the varying sizes that the eggs were not all laid by one bird . . . Whether the cracks in the two whole Honeyguide eggs were the work of the last Honeyguide to lay in the nest or were the result of the Scimitar-bill damaging the eggs with its claws, is not known, but the latter eventuality seems the more probable, as there were no holes comparable with peck marks. The whole Scimitar-bill egg appears to have been damaged in a like manner, but the broken one is more probably the work of a Honeyguide. The small size of the Scimitar-bill clutch would appear to be due to the Honeyguides removing the other eggs.
>
> That the white eggs in the nest belong to the Honeyguide is beyond question, for the chick that hatched from the one egg was without doubt a Honeyguide chick. It has zygodactylous feet and the short stout bill was armed at the tips with tiny needle-sharp transparent yellowish hooks, the upper fitting to the left of the lower when the bill is closed. The translucent flesh-coloured skin was devoid of all trace of feathers; it was totally blind and more or less helpless.
>
> Although in five years of bird watching in the district I have never seen any species other than the Greater Honeyguide (*Indicator indicator*), I felt it advisable

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[24] *Irrisor erythrorhynchus guineensis* Reichenow, Ornith. Monatsb., vol. 10, p. 78, 1902. (Portuguese Guinea to Niger.)

to leave the chick in the nest in order to confirm the identification when it was fully fledged, and blocked up the slit I had made in the tree with a piece of bark. On hearing of this discovery, Dr. Roberts expressed a desire to have the chick as a specimen whilst it still had the hooks on its beak, so that after about 10 days the nest was revisited. The piece of bark had fallen away in the meantime, yet the Hoopoes continued feeding the fully exposed chick. In the 10 or 11 days since hatching, it had grown surprisingly rapidly. The two hooks were still intact, and did not appear to have increased in size, although the bill had now nearly assumed its adult size and shape. Feathers were sprouting from all over the body, and those of the throat were a pale lemon-yellow, confirming the identity as a Greater Honeyguide, this being endorsed by Dr. Roberts. The eyes were open and the feet still retained their zygodactylous habit.

The chick is now preserved in spirits in the Transvaal Museum, Pretoria.

Lybius torquatus torquatus (Dumont). Black-collared barbet.

Bucco torquatus Dumont, Dictionnaire des sciences naturelle, ed. Levrault, vol. 4, p. 56, 1817. (Brazil, error=South Africa, Goffin *in* Schlegel, Muséum des Pays-Bas, No. 15, Buccones, p. 4, 1863.)

This barbet is one of the most frequently imposed upon hosts of the lesser honey-guide, and has been recorded, a fewer number of times, as a victim of *Indicator indicator* as well. The pertinent data are the following.

Layard (1875–1884, pp. 168–169) lists this barbet as a victim of the greater honey-guide.

A. Roberts (1939, pp. 100–102) writes that in the Transvaal Museum is a set of four eggs of this barbet and one of *I. indicator*, collected at Pongola River, Zululand, December 2, 1920. This seems to be the same case mentioned by Priest (1948, pp. 63–64).

A set of four eggs of the barbet with one of the greater honey-guide, taken at Umvukwe Ranch, Banket, Southern Rhodesia, by B. M. Neuby-Varty, is now in the collection of Mr. C. H. Jerome, of Estcourt, Natal.

Further evidence suggestive of mutual relationships between the barbet and the honey-guide may be sensed from the fact that near the Mtetezi River, Northern Rhodesia, Winterbottom (1936, p. 775) saw one of these barbets chasing a greater honey-guide, and in Natal I was told by Mr. H. M. Millar that he once saw a "pair" of the honey-guides at a nest hole of this barbet. The barbet chased away the male honey-guide, whereupon the female honey-guide slipped into the nest. The nest being inaccessible, Mr. Millar was not able to tell definitely if the honey-guide laid an egg in it or not.

It may be mentioned that in at least one of the known cases of the yellow-throated sparrow serving as a host of the greater honey-guide the birds were using an old nest hole of a black-collared barbet.

Tricholaema leucomelan leucomelan (Boddaert). Pied barbet.

Bucco leucomelas Boddaert, Table des planches enluminéez d'histoire naturelle, p. 43, 1783. (Cape of Good Hope, ex Daubenton, Planches enluminées, pl. 688, fig. 1.)

Plowes (1944, p. 91) found a nest of a pied barbet near Bloemhof, South Africa, on January 11, 1942, containing two eggs of the barbet and one smaller one (18.6 by 15.5 mm.), apparently of an *Indicator.* Roberts suggests that this egg may have been laid by a greater honey-guide, but the identification is very uncertain, and the record must therefore be looked upon as unsatisfactory.

I know of but one other record, and it has incomplete data. In the collection of the National Museum of Southern Rhodesia, at Bulawayo, is a set of three eggs of the pied barbet with one attributed to the greater honey-guide collected at Adelaide, Cape Province, in October or November 1919.

The pied barbet is a frequent victim of the lesser honey-guide, *I. minor.*

Pogoniulus pusillus pusillus **(Dumont).** Red-fronted tinkerbird.
Bucco pusillus DUMONT, Dictionnaire des sciences naturelle, ed. 1, vol. 4, p. 50, 1805. (Sandag=Sundays River, Cape Province.)

One doubtful record.

This little barbet is recorded by Layard (1876, p. 170) as a victim of the greater honey-guide. The small size of the barbet might cause one to wonder if the honey-guide may not have been *I. minor.* As a matter of fact, Finn (1919, p. 198) apparently attributes this record to *I. minor.*

Pogoniulus bilineatus alius **Friedmann.** Golden-rumped tinkerbird.
Pogoniulus bilineatus alius FRIEDMANN, Auk, vol. 47, p. 86, 1930. (Nairobi.)

Jackson (1938, pp. 719–720) states that van Someren has taken an egg of the greater honey-guide from a nest of this barbet. This is certainly a very small host and I cannot help but wonder if a greater honey-guide could get into its nest to lay there. Van Someren (1916, p. 238) has recorded what seems to be the same record under the name *Barbatula jacksoni.*

Trachyphonus vaillantii vaillantii **Ranzani.** Crested barbet.
Trachyphonus vaillantii RANZANI, Elementi di zoologia, vol. 3, pt. 2, p. 159, 1821. (South Africa ex Levaillant.)

Known as a victim of the greater honey-guide in the eastern Transvaal and in Southern Rhodesia. At Komati Poort, eastern Transvaal, Mr. Victor Pringle (in litt.) informs me that he has found the crested barbet to be parasitized in November.

At Umvukwe Ranch, Banket, Southern Rhodesia, Neuby-Varty found a nest in October 1945 containing one egg of the honey-guide and three of the barbet, all hard set. The nest was in a stump sticking out of a tree; the top of this stump broke off just above the nest entrance, exposing the eggs. Returning four days later he found all four eggs had hatched a day or two before; four days later still he found that the young parasite had ejected the young barbets, which he found alive and uninjured on the ground below. He returned them to the nest and stayed up in the tree to watch what might happen. He remained there half an hour and nothing took place; he then climbed down and had not been down five minutes when the young barbets were ejected one by one at intervals of about five minutes between them. He picked them up and found them living and unharmed and then put them back again and removed the young honey-guide. The young barbets eventually grew up.

Campethera taeniolaema taeniloaema **Reichenow and Neumann.** Fine-banded woodpecker.

Campothera taeniolaema REICHENOW AND NEUMANN, Ornith. Monatsb., vol. 3, p. 73, 1895. (Eldoma, Rift Valley.)

Van Someren informs me (in litt.) that on two occasions he found single chicks of the greater honey-guide in nests of this woodpecker in the highlands of Kenya Colony.

Campethera nubica **(Boddaert).** Nubian woodpecker.

Picus nubica BODDAERT, Tables des planches enluminéez d'histoire naturelle, p. 41, 1783. (Nubia, ex Daubenton, Planches enluminées, pl. 667.)

Two races of the Nubian woodpecker are recorded as victims of the greater honey-guide.

Van Someren (1916, p. 234) found an egg of the greater honey-guide in a nest of the nominate race of this woodpecker at Mubendi, Uganda, September 28, 1910. Unfortunately no information is given as to the rest of the contents of the nest. Recently (in litt.) van Someren has informed me that in Uganda, in central Kenya Colony, and in the Suk district he has found this bird to be one of the most frequent victims of the parasite during April and May, and that in the coastal areas of Kenya he has found the pale race of this bird, *Campethera nubica pallida* (Sharpe),[25] to be victimized by the greater honey-guide. Unfortunately no more exact data are available on these observations.

Campethera abingoni **(Smith).** Golden-tailed woodpecker.

Chrysoptilus abingoni A. SMITH, Report of the expedition for exploring Central Africa, p. 53, 1836. (Port Natal, Durban.)

Three subspecies of the golden-tailed woodpecker are reported as hosts of the greater honey-guide.

The southern, nominate race of this woodpecker is known to be parasitized by honey-guides, but the identification of the parasite is uncertain. Chubb (1914, p. 65) reports a set of three eggs of this bird and one of a honey-guide taken at Umzinto, South Africa, in November 1905 by A. D. Millar. The *Indicator* egg from Umzinto measures 22.3 by 19.3 mm. and would therefore seem to agree with the eggs of *I. indicator* and of *I. variegatus.* Inasmuch as the former is so very much commoner and more widespread than the latter species, the record is here tentatively referred to the greater honey-guide. Belcher (1930, p. 171) also records a honey-guide egg from a nest of this woodpecker collected in Nyasaland on September 29. This record is also only attributed to *I. indicator.*

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[25] *Dendromus pallidus* Sharpe, Ibis, ser. 8, vol. 2, p. 638, 1902. (Lamu.)

Of the subspecies *smithii* (Malherbe) [26] only one record is known to me, kindly communicated by its discoverer, B. M. Neuby-Varty, who found a nest of this woodpecker early in October 1949 near Marandellas, Southern Rhodesia, containing one hard set egg of the greater honey-guide and two pecked eggs of the woodpecker.

The Mombasa race of the golden-tailed woodpecker, *Campethera abingoni mombassica* (Fischer and Reichenow),[27] is reported as a host of the greater honey-guide by van Someren (in litt.), who writes me that he has found parasitized nests in the coastal area of Kenya Colony, each containing a single chick of *I. indicator.*

Mesopicos goertae centralis Reichenow. Uganda gray woodpecker.

Mesopicos goertae centralis REICHENOW, Ornith. Monatsb., vol. 8, p. 59, 1900. (Ndussuma, west of Lake Albert.)

In central Uganda, van Someren (in litt.) found this woodpecker to be parasitized by the greater honey-guide.

Hirundo albigularis Strickland. White-throated swallow.

Hirundo albigularis STRICKLAND, *in* Jardine, Contributions to ornithology, text p. 17, pl. 15, 1849. (South Africa.)

Ivy (1901, p. 20) saw a greater honey-guide leave a nest of this swallow. He examined the nest and found it to contain two eggs of the swallow and one of the *Indicator.*

Gill (1945, p. 91) lists the white-throated swallow as one of the commonest fosterers of the greater honey-guide in South Africa, but if this statement has any further basis than Ivy's lone record I have not been able to learn of the data. This swallow is also mentioned as a host of the greater honey-guide in the Albany Museum's "Guide to the Vertebrate Fauna of the Eastern Cape Province" (1931, p. 159).

Hirundo semirufa gordoni Jardine. West African rufous-chested swallow.

Hirundo gordoni JARDINE, Contributions to ornithology, p. 141, 1851. (West Coast of Africa, i.e. Gold Coast.)

At Abeokuta, southwestern Nigeria, on June 4, 1944, Serle (1950a, p. 88) found a nest of this swallow containing as its sole occupant an almost fully fledged young greater honey-guide. The nest, a solitary one on the rounded roof of a road culvert, was of the usual retort shape, lined with feathers. The pair of foster parents was seen bringing insects to the nest.

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[26] *Picus (Chrysoptilopicus) smithi* Malherbe, Rev. Zool. (Soc. Cuvier), vol. 8, p. 403, 1845. (South Africa.)

[27] *Picus (Campothera) mombassicus* Fischer and Reichenow, Journ. Ornith., vol. 32, p. 262, 1884. (Mombasa.)

Hirundo cucullata Boddaert. Larger stripe-breasted swallow.

Hirundo cucullata Boddaert, Table des planches enluminéez d'histoire naturelle, p. 45, 1783. (Cape of Good Hope, ex Daubenton, Planches enluminées, pl. 723, fig. 2.)

There is a set of eggs in the Transvaal Museum collected at Grahamstown, Cape Province, in January 1896 containing two eggs of the host and one of the parasite (A. Roberts, 1939, p. 100–102).

Priest (1948, pp. 63–64) lists this swallow as a victim of the greater honey-guide, probably on the basis of the above record.

Mr. F. G. Turberville, at Highlands Rail in Cape Province, writes (in litt. to C. J. Skead) that for several years the greater honey-guide victimized "one of the larger stripe-breasted swallows, and, like the cuckoo, got rid of the swallow chicks at some stage, finally coming out of the nest and hanging around on a nearby tree for a couple of weeks, making the plaintive cry that most young chicks make; all this time the swallows fed it hard and often. Swallows know that the guide is a parasite and go for her on sight if she comes near the nest; last year one tried to get to our swallows on the front stoop, but she was chased so vigorously so often that she gave it up."

On subsequent questioning, Mr. Turberville recalled the yellowish breast of the young parasite, thus eliminating any doubt as to whether the species was really *I. indicator.* He further related (to C. J. Skead, who passed the information on to me) that the swallows always nested in an old ironing-room, and that when the young honey-guide emerged from the nest it usually perched on a large *Rhus* bush about 15 yards from the nest, and remained there cared for by the swallows for "about a week."

Near Pietermaritzburg, Natal, on March 5 Walter J. Lawson (in litt. to C. J. Skead) found a nest of this swallow containing two dead chicks largely eaten by ants. He felt, from the maxillary hook still discernible on one of them, that it was probably a young greater honey-guide.

Monticola rupestris (Vieillot). Cape rock thrush.

Turdus rupestris Vieillot, Nouveau dictionnaire d'histoire naturelle, vol. 20, p. 281, 1818. (Near Cape Town, i. e., Table Mountain.)

One record, of doubtful accuracy.

The late H. W. Bell-Marley found a nest of this thrush at Vryheid, South Africa, October 25, 1910, containing one egg of the greater honey-guide and two eggs of the builder. This set is now in the Transvaal Museum (A. Roberts, 1939, pp. 100–102). If correct, this is a most unusual record as the thrush builds an open nest in the open.

Roberts accepts the record; however, there is some doubt attached to it, as I have recently learned that Bell-Marley often acquired sets of eggs from native assistants, and this may have been such a one.

Priest (1948, pp. 63–64) lists a set of three eggs of the rock thrush and one of the greater honey-guide collected October 20, 1910. This may well refer to the same nest as the above.

Myrmecocichla aethiops cryptoleuca **Sharpe.** Kenya anteater-chat.

Myrmecochichla cryptoleuca SHARPE, Ibis, ser. 6, vol. 3, p. 445, 1891. (Kikuyu.)

Two records, both from Kenya Colony, and both not as completely authenticated as to the species of *Indicator* as one might wish.

Belcher (1942, p. 93) found a nest of this anteater-chat in a tunnel on March 24, 1940. It contained four eggs of the builder and one that was probably of *I. indicator*, an assumption that may be looked upon as correct. A week later Belcher found another nest, also with four eggs of the chat and one presumed to be of a greater honey-guide. In the first instance, three of the four chat's eggs were dented as if pecked; in the second case all the chat's eggs were so damaged.

Myrmecocichla formicivora formicivora **(Vieillot).** Cape anteater-chat.

Oenanthe formicivora VIEILLOT, Nouveau dictionnaire d'histoire naturelle, vol. 21, p. 421, 1818. ("Pays des Cafres," i. e. eastern Cape Province; Sundays River, ex Levaillant, Histoire naturelle des oiseaux d'Afrique, vol. 4, pls. 186, 187, 1805.)

Two records.

In the Albany Museum's "Guide to the Vertebrate Fauna of the Eastern Cape Province" (1931, p. 159) it is stated that an egg of the greater honey-guide was collected from a nest of this chat by S. B. Fowlds. This set is not now to be found; it is possible that if it was in the Albany Museum's collection at one time, it may have perished in the disastrous fire that ravaged that institution about 12 years ago. At any rate, the exact date and locality are not traceable.

A second record, fortunately with data, has come to me from D. C. H. Plowes (in litt.). At Willow Grange, Natal, on December 18, 1951, he found a nest of this chat containing four eggs of the chat and one of the greater honey-guide. There were small holes resembling claw marks on two of the four chat's eggs. Plowes writes me that the honey-guide "must have wandered quite a long way in search of a nest, as the nest was in a donga on the open flats about a mile from where honey-guides are normally seen, which is down in a deep thorny valley."

This species, like *M. aethiops*, builds its nest in a tunnel in the slanting roof of an aardvark burrow, a location also favored by the little bee-eater, *Melittophagus pusillus*, one of the frequent hosts of the greater honey-guide.

Cinnyricinclus leucogaster verreauxi **(Bocage).** Southern violet-backed starling.
Pholidauges verreauxi BOCAGE, *in* Finsch and Hartlaub, Die Vögel Ost-Afrikas, p. 867, 1870. (Caconda.)

I know of but one record, not certainly identified as to the parasite (either *I. indicator* or *I. variegatus*). A. Roberts (1939, pp. 100–102) writes that a set of three eggs of the starling and one of the honey-guide collected on the Pongola River, Zululand, November 8, 1933, is now in the collection of the Transvaal Museum. This record is also mentioned by Priest (1948, pp. 63–64).

Lamprocolius nitens culminator **Clancey and Holliday.** Eastern Cape red-shouldered glossy starling.
Lamprocolius nitens culminator CLANCEY AND HOLLIDAY, Ostrich, vol. 22, No. 2, p. 114, October 1951. (Addo Bush, near Port Elizabeth, Cape Province, South Africa.)

A single instance has come to my attention, a nest containing one egg of the red-shouldered starling and one of the greater honey-guide found at Belmont Valley, near Grahamstown, Cape Province, in December 1950 by Michael Cooke. I am indebted to C. J. Skead for this record, which came to him from Dr. John Hewitt of the Albany Museum.

Lamprocolius chalybeus sycobius **Hartlaub.** Southern blue-eared starling.
Lamprocolius sycobius HARTLAUB, Journ. Ornith., vol. 7, p. 19, 1859. (Tette.)

In the collections of the Transvaal Museum is a set of two eggs of this glossy starling with one of the greater honey-guide (presumably), collected at Pietersburg, Transvaal, on November 11, 1933 (A. Roberts, 1939, pp. 100–102). The same instance is mentioned by Priest (1948, pp. 63–64). Winterbottom (1951, p. 31) lists this starling as a host of the greater honey-guide.

Spreo bicolor **(Gmelin).** Pied starling.
Turdus bicolor GMELIN, Systema naturae, vol. 1, pt. 2, p. 835, 1789. (Cape of Good Hope.)

This starling is a common victim of the greater honey-guide in Natal and the eastern Cape Province.

Mr. R. E. Symons collected three parasitized sets of eggs near Howick, Natal, on September 16, October 5, and October 30. Each consisted of four eggs of the starling and one of the honey-guide. Gibbs (in litt.) informs me that at Kasuga, near Port Alfred, on November 12 he found a nest containing six eggs of the starling and one of the honey-guide. He saw the starling driving the honey-guide out of the nest tunnel before he dug it out.

A. Roberts (1939, pp. 100–102) records a set of two eggs of the host and one of the greater honey-guide taken at Fish River, Cape Province. This set is now in the Transvaal Museum.

Haagner and Ivy (1907b, p. 103) consider *Spreo bicolor* the usual host in the Albany district, Cape Province, and illustrate a parasitized set of eggs in which the starling eggs were broken by the parasite.

Masterston (1916, p. 131) records still another nest with three eggs of the starling and one of the honey-guide.

Priest (1948, pp. 63–64) lists the pied starling as a victim of the greater honey-guide, as does the Albany Museum's "Guide to the Vertebrate Fauna of the Eastern Cape Province" (1931, p. 159). Lydekker (1916, p. 150) states that the greater honey-guide parasitizes this starling, but gives no further details.

Plowes once found a full grown chick of the greater honey-guide in a nest of a pied starling at Willow Grange, near Estcourt, Natal.

Stuckenberg (in litt.) found the pied starling to be parasitized each year from 1945 through 1947 at Schoenmaker's Kop, about five miles from Port Elizabeth.

Petronia superciliaris superciliaris (Blyth). Yellow-throated sparrow.

Gymnorhis superciliaris Blyth, Journ. Asiatic Soc. Bengal, vol. 14, p. 553, 1845. (South Africa.)

At "Gameston," a farm 15 miles southwest of Grahamtown, Albany district, southeastern Cape Province, Skead (1951, p. 60) observed the fortunes of a pair of yellow-throated sparrows that were nesting in a deserted hole of a black-collared barbet. On December 12 he heard what sounded like the constant purring sound of a honey-guide chick in the nest, and opened it and found his surmise to be correct. The honey-guide was the sole occupant of the nest and was estimated to be about 16 days old. It left the nest on January 5. Skead writes that he did not observe any adult honey-guides about the nest at the time of egg-laying, and that the young parasite must have disposed of the young sparrows in some way because there was no sign of them or of their dead bodies either in the nest or on the ground nearby.

At Kei Road, Cape Province, Gordon Ranger collected a set of two eggs of the yellow-throated sparrow and one of the greater honey-guide. This set is now in the East London Museum. The same observer watched another instance of this sparrow as a foster parent of the greater honey guide, the details of which are given in our discussion of the postnestling stage of the parasite. As in the case observed by Skead, the young honey-guide was the sole occupant of the nest when first seen.

On December 27, 1951, at "Assegai River Farm," two miles from Seven Fountains, Albany district, Cape Province, Skead found a nest of this sparrow containing a young greater honey-guide.

What seems to be one of the earliest recorded instances of the yellow-throated sparrow as a host of the honey-guide is given by Lydekker (1916, p. 150), who mentions a young honey-guide (of uncertain species, however) taken from a nest of this sparrow.

Passer griseus gongonensis (Oustalet). Parrot-billed gray-headed sparrow.
Pseudostruthus gongonensis Oustalet, Le Naturaliste, ser. 2, vol. 4, No. 90, p. 224, 1890. (Gongoni, near Mombasa.)

A single record has come to my attention. It was kindly sent to me by Sir Charles F. Belcher. On July 19, 1944, at Muthaiga, a suburb of Nairobi, he was shown a fledgling greater honey-guide that had been placed in a wooden box on a veranda where it could be fed by its foster parents. He saw the latter, a pair of parrot-billed sparrows, come and feed the young *Indicator*. On making inquiries about the nest from which it had been taken, he was shown a nest of a mosque swallow with a tubular entrance under the eaves at the back of the 2-story house of the friend who had asked him to see the bird. Sir Charles broke off the tubular entrance and found that the nest had been relined with grass by the sparrows; it contained one egg of the host, quite dried, but showing a peck hole similar to those in eggs in nests of other victims of the greater honey-guide.

Questionable Host Records

Aside from the species known with greater or less evidence as hosts of this honey-guide, a number of other birds have been mentioned in the literature as victims of its parasitic habits. None of these are substantiated by any preserved or recorded evidence and all seem unlikely. However, our knowledge is not yet on such firm foundation as to enable us to rule out these cases merely because they seem unlikely. They are therefore given below with the necessary qualifying remarks.

The earliest mention of the fact that the honey-guides are parasitic in their breeding habits is that given by Hartlaub (1854, p. 417) on the basis of observations communicated to him by the Verreaux brothers. They recorded finding eggs or young of the greater honey-guide (listed by them as three distinct species on the basis of the juvenal, adult male, and adult female plumages) in nests of two species of woodpeckers (*Campethera nubica* and *Dendropicos fuscescens*),[28] an oriole (*Oriolus monachus larvatus*), two bulbuls (*Pycnonotus capensis* and *Andropadus importunus*) and two shrikes (*Laniarius ferrugineus* and *Dryoscopus cubla*). While the two woodpeckers may be correct, I doubt very much that the open-nesting birds—such as the orioles, bulbuls, and shrikes—can be looked upon as validly identified hosts. Aside from the great improbability that the Verreaux brothers should have had so many observations at variance with the experience of all subsequent observers, their other notes (as recorded by Hartlaub) on the habits of the honey-guides are obviously erroneous. I can only hazard a possible guess that in the case of the bulbuls and shrikes the supposed *Indicator* eggs may have been eggs of the southern Jacobin cuckoo, *Clamator jacobinus serrator*. A further doubtful statement is recorded by Finsch and Hartlaub (1870, p. 347) to the effect that they had a note in Verreaux's handwriting stating that he found a nest of *Dryoscopus cubla* containing two young shrikes and one young *I. major* (= *I. indicator*) which had grown up together! The Verreaux brothers' observations have been quoted not only by Finsch and Hartlaub but also by Des Murs (in Lefebvre, 1850); fortunately they have been ignored by recent writers.

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[28] Benson (1953, p. 45) lists *Dendropicos fuscescens* as a host in Nyasaland but leaves the record open to doubt as to identification

A South African drongo, *Dicrurus adsimilis adsimilis*, figures in the literature as a host of the greater honey-guide but the evidence is based on a single record which seems to me without value. Ivy (1901, p. 21), at Blue Krantz, South Africa, saw a greater honey-guide pursued by two drongos whose nest was on the top of a tall euphorbia. He writes that he "could distinctly make out the transparent egg of the Honey-guide along with the more opaque-white eggs of the Drongo, of which there were 3." This record is accepted by Roberts (1939, pp. 100–102); and Priest (1948, pp. 63–64) writes that drongos are suspected of being hosts of this honey-guide. Gill (1945, p. 91) also lists "the drongo" as a victim, as does the author of the Albany Museum's "Guide to the Vertebrate Fauna of the Eastern Cape Province" (1931, p. 159). Aside from the fact that honey-guide eggs are not "transparent," there is no indication that Ivy even climbed up to and examined the nest and its contents. The mere fact that the drongos were chasing a honey-guide is no evidence that the latter had laid an egg in their nest. It would seem that this record is one that had better be deleted as having no established basis.

To these may be added some very inconclusive notes on two other birds not otherwise known to be affected by the honey-guides—the fiscal flycatcher, *Sigelus silens*, and the scarlet-breasted sunbird, *Chalcomitra senegalensis*. Of the former, H. A. W. Bladen, of Cradock, Cape Province, writes me that once in 1939 he saw a fledged young honey-guide together with a pair of fiscal flycatchers. He was able to observe it closely at very close range (about 8 feet), but did not see it actually either beg for food from the flycatchers or receive any attention from them, although he had the birds under observation for a number of minutes. He felt that the birds were definitely associated and were not in the tree merely by coincidence. Of the sunbird, Priest (1931, p. 66), at Wedza, near Marandellas, Southern Rhodesia, found an adult male *Chalcomitra* together with a fully fledged immature *Indicator indicator*. At his approach they flew to another tree and alighted near each other again. He then collected the young honey-guide. Again, as in the case of the flycatchers, there are no observations to prove any parent-offspring relationship. Priest (1936, p. 102) mentions this honey-guide as parasitizing a nest of the black tit, *Parus niger*, at Wedza, Southern Rhodesia. This record he subsequently reidentified (in litt.) as referring to the lesser honey-guide (*Indicator minor*).

Development of the Nestling

The greater honey-guide when newly hatched is blind, helpless, devoid of any trace of feathers, has a translucent flesh-colored skin and a pair of small, very sharp, transparent yellowish hooks on the tips of the mandibles, the upper one fitting to the left of the lower one when the bill is closed. Plowes (1948) found such a newly hatched bird possibly one day old, and revisited it 10 days later when he noted: "In the 10 or 11 days since hatching, it had grown surprisingly rapidly. The two hooks were still intact, and did not appear to have increased in size, although the bill had now nearly assumed its adult size and shape. Feathers were sprouting from all over the body, and those of the throat were a pale lemon-yellow . . . The eyes were open."

Skead (1951, pp. 60–61) describes a nestling that he estimated to be about 16 days old but which (in light of Plowes' description of a 10- or 11-day-old chick) may have been a day or two younger.

> The feathers were just emerging from the pointed quills all over the body; the back and wings were olive-brown; rump white; abdomen and breast yellowish white, and throat bright yellow; eye about a quarter open . . .
>
> On the "heel" of the tarso-metatarsus was a little rosette of scales similar to that on a Black-collared Barbet . . . But, most interesting, were the hooks on the tips of both mandibles. The base of the upper hook, where it joined the beak, extended slightly over the upper mandible and, protruding therefrom, in a position where the egg-tooth would occur in a normal beak, was a minute conical protuberance which had probably served the purpose of an egg-tooth.
>
> The chick left the nest on January 5 and never returned . . . If the chick was 16 days old when I first saw it, then the nestling period would have been about 40 days which is close to the 38 days of the Lesser Honeyguide. Therefore, when they leave the nest the birds can be considered as well-developed.

During a large part of its nest life the young honey-guide keeps up a constant purring sound. As Skead puts it, the call of the nestling "is husky and perpetual just like that of the Lesser Honeyguide nestling . . . not dissimilar to the guiding call of the adult but of course undeveloped. It can be heard, greatly accelerated and intensified, 75 yards from the nest whenever a foster-parent approaches with food. This happens during the later days in the nest."

Ejection of Nest Mates

That the nestling greater honey-guide ejects the other young or eggs in the nest is recorded by many statements in the literature, but in every one of these cases the authors were either assuming that this had happened because the young parasite was the sole occupant of the nest or were merely repeating what had been said by earlier writers on equally inferential grounds. The danger of making such an assumption is obvious when we realize that the young *Indicator* may only starve out any competitors in the nest, and that their dead bodies may be removed later by the parent birds as part of normal nest sanitation. However, it is now possible to state positively that ejection by the young parasite does take place, although how frequently or even how regularly this may transpire is unknown as yet.

The one case in which ejection has been proved is in the following account, kindly supplied me by its observer, B. M. Neuby-Varty. In early October 1945, at Umvukwe Ranch, Banket, Southern Rhodesia, Neuby-Varty found a nest of the crested barbet, *Trachyphonus vaillantii vailantii*, containing three eggs of its own and one of the greater honey-guide. The nest cavity was in a hole about 4 feet from the top of a stump of a branch sticking out of a tree about 8 feet from the ground. The top of this stump broke off at the entrance to the nest exposing the eggs, all of which were hard set and which therefore were not collected (fortunately). Four days later Neuby-Varty inspected the nest again and found that all the eggs had hatched a day or two before; on revisiting the nest four days later again he found that the young honey-guide was the sole occupant of the nest while the three young barbets, alive and unharmed, were on the ground below. He picked them up, found no bruises or scratches on them, and replaced them in the nest and stayed up in the tree to see what might take place. Nothing happened for about half an hour, and he climbed down again, but was not on the ground more than a few minutes when one of the young barbets was pushed over the rim of the nest and fell down to the earth. About five minutes later the second young barbet was similarly ousted, and five minutes later again the third one was ejected. From his position on the ground he could not see exactly how the young honey-guide did it, but he told me that he could see what might have been either the mandibular hooks or the claws of the young parasite grasping the rim of the nest when ejecting the barbets. (I doubt if the small and translucent mandibular hooks could be seen at a distance of even a few feet; furthermore, there is no real certainty that the claws, if claws they were, were those of the honey-guide and not of the young barbet struggling against eviction.) Unfortunately from our standpoint, the barbets were of more interest than the honey-guide to Neuby-Varty and he replaced the three nestlings and removed and killed the young parasite.

This most interesting case does, at least, prove that honey-guide chicks will eject their nest mates if they can, and that this takes place within a week after hatching. (Unfortunately, as Neuby-Varty was away when the eggs hatched, the exact age of the birds at the time of ejection is not known, though they must have been not less than five or more than six days old at the time.) In conversation about this observation Neuby-Varty informed me that he thinks that ejection is usually not done, or needed, as in his experience the laying honey-guide usually pecks the hosts' eggs, which then do not hatch. As shown in our discussion of the egg-laying habits, this pecking is by no means universal, being, in fact, quite uncommon or even unknown in the experience of some observers. Therefore, it may well be that the occasion, or at least the stimulus for ejecting, occurs not infrequently. In many nests it would seem physically impossible for the young honey-guide to oust its nest mates. In this connection it may be recalled that in one of the parasitized nests of an African hoopoe, *Upupa africana*, discussed under that species, there was a shrivelled dead nestling hoopoe together with a newly hatched, still naked, young honey-guide. In another nest more suitable for ejection the nestling hoopoe might well have been evicted.

Young of the greater honey-guide, when hatched, have a pair of sharp, almost needlelike hooks on the bill. It has been assumed by several writers that these are used by the chick as "weapons" with which to destroy the other young or eggs in the nest, but it must be stated that no one has yet seen the young of the greater honey-guide use them, although the nestling lesser honey-guide certainly does, and that in the case of the young crested barbets the ejected birds revealed no marks that might be attributed to these very sharp hooks. We need further direct observational data. It is quite possible, for example, that in the case described above they may have been used not on the body of a nest mate about to be ejected but to grip the nest wall to give the young ejector a firm hold while pushing out its unwanted companion.

Haagner (1911) describes the hooks on a young greater honey-guide "fully fledged and ready to fly"(!). He put this bird in a cage where its foster parents fed it through the wire mesh. After a few days the chick lost one of the hooks (the lower, or mandibular one) and Haagner then killed it to preserve it as a museum specimen while it still had at least one of the hooks attached. He surmised that these hooks probably fall off upon the bird attaining its full growth (not really "maturity" as he inadvertently expressed it).

There seems to be some variation in the duration of these hooks, as van Someren informs me (in litt.) that he found no sign of them in a nestling *Indicator indicator* 10–14 days old.

The Postnestling Stage

A most interesting and informative case history of the postnestling stage is the following, kindly related to me in detail by its observer, Gordon A. Ranger. On the farm "Gleniffer," near Kei Road, eastern Cape Province, on December 27 he found a nest of a yellow-throated sparrow, *Petronia superciliaris,* containing as its sole occupant a fully plumaged, well-developed chick of the greater honey-guide. The young parasite appeared at the opening of the nest hole at and after being fed at each visit of the foster parents, calling lustily at the approach of the sparrows with what Ranger describes as a "juvenile rendering of the chattering (guiding) call of the adult." When he approached the nest hole the bird eyed him for a short time and then withdrew out of sight into the nest chamber. In following the fortunes of this bird, Ranger found that only one of the sparrows fed it; this one is called the female in the subjoined data, but this is only an assumption, and it was not definitely proved by subsequently collecting the bird. From here on I merely transcribe Ranger's words.

Young honey-guide fed at nest hole only by female sparrow. Male sparrow accompanied female on all her moves to and from the nest-tree, both during nest-building, weeks earlier, and while feeding the young honey-guide, but made no contribution either in nest materials or in food until, on December 28, he disappeared. On this date the female sparrow chased an adult *Indicator indicator* from near the nest and pursued it until well away. The honey-guide did not return.

December 31: 8:15 a. m.—Commotion at the sparrow's nest. The missing sparrow had returned and the young *Indicator* had vacated the nest and was perched nearby crying at the expectation of food. A sparrow (male) remonstrated at the presence of a stranger (the young honey-guide) so near to the nest and strove to drive it away. The approach of the sparrow, however, served only to excite the young honey-guide, causing it to increase its cries and to open its bill wide, but instead of receiving the expected food it was assaulted directly by the male sparrow who used its claws on the young bird. Further attacks followed and then the sparrow closed with the honey-guide which slowly swung around on its perch with the sparrow clinging to its head, and in this fashion both fluttered to the ground where the attacking continued. Both the sparrows *apparently* were doing the "mobbing" but only one can have been actually aggressive as subsequent events proved.

When the attack on the ground had ceased, Ranger captured the honey-guide and, after examining it, replaced it in the tree. The young bird was very mature-looking except for the shortness of its tail, and was fat and heavy. In the tree it chose another perch, using its wings somewhat. When the two sparrows returned it was again "mobbed" and one sparrow renewed the assault, bearing its victim to the ground. Here it sat beneath a shrub and the sparrows stood by for some time and then moved off. Nothing new developing, Ranger then advanced to put the honey-guide back in the tree but it flew off and rose up into a tall tree 30 yards away. Shortly afterward when the sparrows settled in this tree, the young honey-guide renewed its food cries. A little later the sparrows flew off, but one returned to feed the young bird which continued to receive food up to 11 a. m. At noon the honey-guide flew to another tree about 30 yards farther away from the nest-tree, and here was watched as it was fed by one of the sparrows.

January 1: 5 a. m.—A sparrow heard noisily calling at various points and later the young honey-guide calling and seen fed repeatedly by the sparrow. At 7 a. m. the young bird had moved to another tree where feeding by a single sparrow continued. In this tree Ranger was able to capture the honey-guide as it slept with its head buried in its feathers. Both of the sparrows were noted at different times on this day, but no attack on the honey-guide was seen. The young bird was active, flitting about among the trees, and at times flew out behind the mother sparrow after being fed. On one occasion it continued to fly out into open space whereupon the mother followed it, but soon the honey-guide, apparently because of the absence of trees before it, turned back and the mother sparrow accompanied it to a perch. As Ranger pointed out in his telling of this case, it was remarkable how the maternal regard in the sparrow persists toward the young parasite, which at the same time seems like an alien to the male sparrow, which attacked it so often.

January 2: Early this morning the young honey-guide was seen being fed as usual by the very attentive foster parent. At about 6:30 a. m. the male sparrow arrived and ruthlessly attacked the young bird in the tree, causing it to scream. The frightened bird fled some distance to a bushy tree closely pursued by the sparrow, and here screamed loudly under renewed onslaught by the latter. During all these attacks and pursuits the female sparrow closely accompanied her mate, and when the attack in the bushy tree ended both flew off to another tree, but shortly the female returned and fed the young honey-guide as before. This attention persisted throughout the rest of the day.

January 3: During the morning the young honey-guide was fed as usual; not heard crying in the afternoon.

January 4: Sparrow (male?) noisy, but not in reference to the young honey-guide. The latter became far more active and lively on the wing, and considerably less responsive vocally to the approach of the sparrows.

January 5: Cries of the honey-guide subdued; its tail feathers now long and its flight wholly adult in manner.

January 6 and 7: Only subdued cries uttered rarely by the young honey-guide, but at 6:20 p. m. on the 7th it flew to a neighboring tree where it met a sparrow and uttered its chattering cry a good deal; later still it was chased relentlessly again by the male sparrow, and fled, crying, in and out among the trees, finally being borne down near to the ground. As before, the female sparrow followed the chase closely. The attack was not renewed a few minutes later when the sparrows again settled near the honey-guide. The latter bird refrained from uttering its hunger cry in contrast to its usual earlier reaction on the arrival of the sparrows.

January 8: Young honey-guide seen for the last time in the forenoon; the sparrows started to build another nest in the same hole where they had reared the honey-guide.

To summarize, the honey-guide continued to be attended, and to be fed, by the foster parent for nine days after leaving the nest. As far as could be told by observation, unimplemented by subsequent collecting, only one of the yellow-throated sparrows (the female) actually fed it, while the other reacted in a hostile manner as though to a strange and unwelcome species.

In the same general area as Ranger's observation, F. G. Turberville noted that a young greater honey-guide was fed and attended by its foster parents, a pair of stripe-breasted swallows, *Hirundo cucullata*, for "about a week" after leaving the nest.

Whether the fully fledged young birds remain solitary for a while or form loose flocks of their own kind is not certain. Near Maktau, Kenya Colony, I twice saw immature, yellow-throated birds in loose companies of seven or eight individuals around herds of hartebeeste and oryx. While I could not see if they were actually feeding, it looked as though they were snapping at insects scared up by the grazing animals.

A. Roberts (1917, p. 261) writes that it has been "noted that Cuckoos and honey-guides sometimes visit their offspring." There are no recorded observations supporting this as far as I know, but many years ago, along with other unreliable statements, the Verreaux brothers (in Hartlaub, 1854, p. 417) claimed that when the young honey-guide is about a month old the adults occupy themselves with feeding it and try to take it away from the fosterer's nest! On March 11, 1944, Miss Clare Robinson of Cape Town (in litt. to Dr. Brockhuysen, who forwarded it to me) saw a young greater honey-guide together with two adult individuals near a tap in her back yard. Further inquiry brought out the fact that no feeding of the youngster by the adults or even food-begging by the young bird was noted. This can hardly, therefore, be looked upon as a significant observation, especially when one considers that the yellow-throated juvenal plumage may be retained for nearly a year or even longer.

The retention of the juvenal plumage is a matter of some interest. Dissection of specimens collected indicates that birds may come into breeding condition while still largely in this plumage and still show no signs of active molting, suggesting that in some cases the fully adult feathering may not be acquired until the birds are two years old. There is, apparently, considerable variation in the duration of the first plumage, but, as it is not yet possible to coordinate all the individual cases satisfactorily, it may be of some use to list the dates of specimens in postjuvenal molt from various parts of Africa.

The following data are culled from the material preserved in the museums of Cambridge (Mass.), Cape Town, Chicago, Copenhagen, Leiden, London, Milan, New York, Paris, Pietermaritzburg, Philadelphia, Pittsburgh, Pretoria, Stockholm, and Washington. South Africa and Bechuanaland: January 6, August 3, 14, 15; Nyasaland: Ruo, September 5; Tanganyika Territory: Iringa, January; Ikoma, July 7; Kenya Colony: Teita, August 29; Uganda: Ankole, July 30; Belgian Congo: Lake Albert, February 15; Guruba River, May 17; Somaliland: Armatch, November 16; Abyssinia: Bogra, February 1; Lake Helone, February 13; Lake Rudolph, March 31; Sudan: Bahr-el-Ghazal, January 28, February 6; Lado, February 11, April 15, French Equatorial Africa: Shari River, July 1, 7; Nigeria: Kafanchan, December 18; Portuguese Guinea: Gunnal, June 6.

That the juvenal plumage is worn for variable periods is shown by the following. In South Africa it is known that the eggs are laid from mid-September to early January, chiefly from late September to mid-December, and the incubation period plus the nestling stage is something less than two months. This would mean that the immature, yellow-throated birds may be expected to be "on their own" from early November to the end of February onward. An immature male taken on the Limpopo River, northern Transvaal, on August 13 was just starting to molt into adult plumage, while another young male, taken at Rustenberg, Transvaal, on January 6, was in a more advanced stage of the postjuvenal molt.

The postjuvenal molt begins on the throat and in the remiges, and seems to end with the feathers of the upperparts.

Guiding

It is in this species that the guiding habit is best developed, far more so than in *I. variegatus*, the only other honey-guide known to lead to bees' nests. The behavior involved in guiding is so unusual and remarkable as to have brought into the literature much descriptive writing, frequently of doubtful value; indeed, the popular conception of guiding is, as intimated in the introduction to this report, overly simplified and generally naively interpreted. The whole subject of guiding has been discussed earlier (on pp. 25–71), and at this point we may merely stress again the fact that there is no occasion whatever to assume anything involving planning or intelligence on the bird's part. The behavior is wholly on an instinctive level, but it is something sought for by the bird, not merely something it does automatically when the necessary stimuli are present. Precisely because so many statements in the literature are poorly phrased with verbal intonations implying foresight or similar mental activity on the part of the honey-guides, I have taken great pains to gather together as many reliable bits of information from other observers and from the literature as possible, and to make specially planned and oriented field observations myself. These are given in the chapter referred to above.

Food and Feeding Habits

Adult: Analyses of the stomach contents of many adult birds collected reveal masses of beeswax, pollen, what seems by the odor to be honey, larval and adult bees, other insects such as winged termites, beetles, and ants, insect eggs, and occasional vegetable matter. Inasmuch as the food obtained from bees' nests has been assumed to be the benefit the bird derives from its guiding behavior, these items deserve special comment. It may be noted, however, that hunger is not necessarily the immediate, driving factor in causing a bird to guide, as evidenced by two examples I shot at the end of guiding trips but before the bees' nests were opened—both specimens proved to have well filled gizzards. In Rhodesia, Plowes also found a guiding bird to have a well filled gizzard. From my own observations, and as far as I can judge by the experience of others communicated to me either directly or in published data, it appears that even in areas where the birds indulge most frequently in guiding they get a large proportion of their food without the aid of human, or, as far as we know, other mammalian associates. This, in turn, implies that not a small number of bees' nests must be available to the birds. In the eastern Cape Province, Skead was shown a place where a swarm of wild bees had started building their combs in a hollow about a foot in diameter in an old tree. The combs were entirely exposed. A lesser honey-guide (*Indicator minor*) was seen nearby, and within a week it had removed it all, either by itself or with assistance from other honey-guides.

Nearby, near Kei Road, Ranger actually observed honey-guides (*Indicator indicator*) entering a wild bees' nest and feeding there. From his place of concealment near the hive he saw an immature bird come to the hive. It very cautiously examined the surroundings and then entered the sawed-off hollow stem that led at a slight incline to the bees' nest three feet within. About a minute later it reappeared at the entrance and paused there with a small piece of straw-colored comb (at least, it looked like comb) in its bill, then flew off a few feet and disposed of the comb, the exact method of dealing with the comb remaining unobserved due to very thick vegetation. From here it went back to the bees' hive and entered it a second time, came out shortly after, and then flew off. A little later an adult male arrived and, after being chased about by some fork-tailed drongos that were eating bees, perched 30 feet above the hive for a long time and then came down, warily moving closer, when it was driven off by a lesser honey-guide (*I. minor*). Some days later more time was spent making observations. A greater honey-guide (either adult female or very advanced subadult bird) arrived at the hive and, after a careful and cautious inspection of the surroundings, went to the entrance, went in about nine inches, came back to the entrance, gave another look about, and then disappeared down the long tunnel. The surge of disturbed bees was distinctly heard. The bird was inside at least 15 seconds, and then out in a hurried flight and went away.

The next day the immature bird referred to at the beginning of Ranger's notes alighted, remained quiet for about 17 minutes, and then dropped down to the hive entrance. It went through the usual semblance of alert searching about of the surroundings, and went in and out of the hive by this entrance two or three times, and through a second similar hole twice, and examined a third entrance hole to the hive before departing exactly an hour and a half after first appearing. The longest time it was inside the hive was 55 seconds. On emerging it wiped its bill but did not bring out any comb.

On three occasions when a greater honey-guide came to the bees' nest in Ranger's presence there was no chattering or other note given by the bird. Ranger also saw *I. minor* and *I. variegatus* at this bees' nest.

These observations make it clear that guiding is not an indispensable factor in their feeding habits. And yet there is not the slightest doubt that the birds eat beeswax regularly and even avidly. Certainly, after a guiding trip to a bees' nest, the guide remains in the immediate vicinity while its followers open up the nest, and before they are gone more than a minute or two it comes down to feed on the bits of comb left strewn about. Not only does the guiding bird itself do this but often other individuals of the same species and even of other, non-guiding species of *Indicator* (such as *minor*) join it to feed on the exposed comb and its contents.

Wax is present in almost all the stomachs examined or recorded. Inasmuch as wax seems to be definitely bound up with the whole guiding behavior of these birds, it is necessary to consider it in such detail as we can, as is done in our chapter on cerophagy (see pp 71–79). While this interest in wax, as such, is unusual in birds, it may be pointed out that in almost all insects, and other arthropods, there is a small amount of wax present on the outer layer of the cuticle, so it follows that all insectivorous birds do swallow wax, even though in very small quantities.

Aside from wax, insects form the main food of the greater honey-guide. I know of no definite observations of honey-guides eating any waxy combs of any insects other than bees. It is true that many years ago Butler, Feilden, and Reid (1882, p. 208) reported collecting an adult female *I. indicator* that was seen "on the ground . . . pecking at a large piece of the comb of a wasp's nest," but it is not stated whether the bird was extracting wasp larvae or eating the comb structure itself. Of the insects eaten, bee larvae and adult bees are the most frequent, and have been found in stomachs of birds taken in all parts of the range from South Africa to Ethiopia. Skead (1951, p. 61) often saw greater honey-guides perching near the entrances to some of his garden beehives but never noticed them feeding there as do the lesser honey-guides. However, as evidenced by the fact that adult bees have been found in their stomachs, they must occasionally feed on them. Actual records of adult bees in the stomach contents of greater honey-guides are at hand from South Africa, Kenya Colony, Belgian Congo, and Ethiopia. Honey also is frequently found in the stomachs of greater honey-guides in all parts of the range.

In Southern Rhodesia I have seen a greater honey-guide catch and eat winged termites in midair in the fashion of a flycatcher, and Chapin has recorded the same in the Belgian Congo. In fact, in the stomach of one bird he counted no fewer than 80 winged termites. Swynnerton (1908, p. 411) also found the bird to eat termites in Gazaland, Southern Rhodesia. Termites from the gizzard of a greater honey-guide shot in South Africa proved to be *Odontotermes* *angustus.* In Ethiopia, Pease (in Ogilvie-Grant, Reid and Pease, 1901, p. 667) found the "crop" of an adult to contain ants and other small insects. Beetle remains have been recorded in a stomach from the Belgian Congo, where Chapin found a variety of insect remains mixed with the wax in practically all of the honey-guide stomachs he examined. In the Mount Elgon area Granvik (1923, pp. 83–84) found stomachs to contain gravel, pebbles, and insect remains. In Ethiopia, Heuglin (1869, pp. 767–769) noted the birds' stomachs held larvae, honey, wax, termite eggs, caterpillars, and bees. In Angola, Bocage found a locust in the stomach of a greater honey-guide. To complete our inventory of the known food items eaten by the adult birds, I may merely add that a specimen shot near Kasempa, Northern Rhodesia, by E. L. Button and now in the Transvaal Museum bears on its label a note to the effect that the "crop contained small seeds and a white substance, possibly berries, and the pulp from one of the local trees." The last mentioned item recalls the case often cited of a woodpecker feeding on the cambium and bast of trees.

I know of only one published note on a greater honey-guide in captivity and on what it ate there. Porter (1927) kept an immature (yellow-throated) bird at large in his room. The first night he fed it on flies mixed with syrup (apparently he thought of honey-guides as honey eaters), but later he fed it soft insects and honeycomb. The bird ate several times its own weight in a week and refused to touch "hard insects or artificial food." A South African aviculturist, W. R. Carthew, informs me that he has kept both greater and lesser honey-guides for over a year on a diet of bread and whole milk with sugar or syrup, supplemented by ants and mealworms. When mealworms were not available, a substitute of raw chopped meat mixed with raw egg was found satisfactory. He occasionally gave the birds pieces of bee comb containing larvae; he saw the birds extract the latter but did not observe them eating the comb itself.

The question has been raised from time to time as to whether or not honey-guides, like certain other parasitic birds, may remove and eat eggs from nests into which they may lay. There are no positive data. Skead (1951, p. 61) saw a male greater honey-guide steal an egg from a nest of a bar-throated bush warbler (*Apalis thoracica*) in the eastern Cape Province. While the bird was not actually seen to eat the egg, the probabilities are that it did so. Inasmuch as the *Apalis* is not the kind of bird that the honey-guide would ordinarily parasitize, and inasmuch as the bird that took the egg was a male (and hence not a potential egg-layer), it would seem that this observation would imply a nest-robbing, egg-eating habit, as such, and not necessarily only as an accessory to parasitic reproduction.

Honey-guides have been observed drinking water on several occasions. I am informed by J. P. Chapin that Rodney Wood, in Nyasaland, noted individuals coming to drink at his birdbath. Mr. P. A. Clancey tells me that when he was in Somaliland with Meinertzhagen a greater honey-guide flew into their tent and perched on the rim of a canvas pail partly full of water. In order to reach the water the bird had to hang almost upside down, and then, after drinking, it had some difficulty in righting itself again.

I have seen loose companies of seven or eight immature (yellow-throated) birds associated with herds of hartebeeste and oryx in Kenya Colony, and a few other observers have had similar experiences. The birds appeared to be picking up food from the grass around these animals just as cowbirds do in the Americas. It is not improbable that they may glean a considerable amount of insect food scared up by the grazing animals, but no data are available.

NESTLING: Skead (1951, p. 61) observed a chick of the greater honey-guide in a nest of a pair of yellow-throated sparrows, *Petronia superciliaris*, and was able to identify a grasshopper among the food given it by its foster parents. On a more recent similar occurrence he noted a mantis and a spider among the food given a young greater honey-guide. Similarly, in West Africa, Serle (1950, p. 88) noted two swallows, *Hirundo semirufa gordoni*, bringing insects to a young *Indicator indicator* in their nest. The gizzard of a nestling greater honey-guide examined by J. S. Taylor in South Africa contained wasps, bees, ants, flies, cicadas, beetles, grasshoppers, and butterflies. Another chick, collected by Benson in Nyasaland from a nest of *Dicrocercus hirundineus*, had its gizzard full of insect remains, among which E. A. Chapin was able to identify 2 grasshoppers, 3 cetoniine scarabs, 2 moths, 1 cicada, 1 asilid fly, 6 other flies, 2 Zygoptera, 12 bees (*Apis mellifera*), 1 anthophorine aphid, 1 eumenine wasp, and 3 polystine wasps. The floor of the nest contained wings of two kinds of butterflies (*Papilio* sp., 1 wing; *Catopsilia florella*, several wings), the bodies of which had evidently been eaten by the young bird.

There seem to be no other available data, but these indicate clearly that the young parasite receives the same sort of food that its fosterers would give their own young—a variety of insects and grubs.

In view of the important role played by wax in the diet of the adult birds, it is worth pointing out that, as far as we know, no honey-guide gets any beeswax until after it has left its foster parents; in other words, until it is practically full grown.

Miscellaneous

Fights with other birds: Heuglin (1869, pp. 767–769) once witnessed an apparently spirited battle between a female greater honey-guide and a coucal (*Centropus* sp.). The latter bird was victorious and drove away the much smaller *Indicator*. The cause or nature of the fight is not described. Recently Skead (1951, p. 58) saw an attack on one of these honey-guides by a brown-hooded kingfisher (*Halcyon albiventris*) when the former came into his garden. A pair of the kingfishers were frequently in and about the garden, but were never seen to attack any of the many other birds there. "Their nesting and sleeping hole was tunneled into an earth bank 150 yards from the garden and their action towards the honeyguide made me wonder whether they had recognized it as an enemy in the way barbets recognize Lesser Honeyguides and weaver-birds recognize cuckoos. The Kingfishers were not nesting at the time." Yet, when a greater honey-guide came into the garden it was promptly and determinedly attacked.

On one occasion Skead saw a larger double-collared sunbird, *Cinnyris afer*, mobbing an adult male greater honey-guide that sat calmly on a twig projecting above the forest canopy, its head drawn down into its hunched-up shoulders, and apparently not unduly disturbed by the excited chattering and fluttering about of the sunbird. On another occasion, near Howick, Natal, early in October, I saw three scimitar-billed wood-hoopoes (*Rhinopomastus cyanomelas*) noisily pursuing a greater honey-guide until all were out of sight.

It is difficult to account for the fact that while many more observers have seen this honey-guide than the lesser one, *I. minor*, the former species relatively rarely has been reported as being attacked by other birds while there are many such instances recorded for the latter species. Similarly, *I. minor* has been observed by numerous naturalists coming to the nest-holes of barbets and other birds and being driven off repeatedly by them, while remarkably few such data are at hand for *I. indicator*. Likewise, whereas *I. minor* frequently attacks and drives away other birds, including some larger than itself, *I. indicator* is not known to do so.

It is well known from many observations of numerous writers that small birds frequently "mob" parasitic cuckoos of various kinds if the latter come near their nests. In the case of certain species of cuckoos, it has been assumed in the literature that this may be due to the hawklike appearance of the intruders, but this possible factor cannot be assumed in the case of the honey-guides. There are, in fact, no data that suggest that this parasite is recognized as a specifically identified "enemy." In the lack of frequent or regular fighting with its host species, the greater honey-guide resembles the American parasitic cowbirds to some extent; this cannot be said for the lesser honey-guide, however. In the present species some comparable hostility has been noted towards the newly fledged young rather than towards its parents. It may be recalled, in the discussion of the postnestling stage, how a yellow-throated sparrow, presumably the male of a pair of foster parents, reacted with hostility to the young *Indicator indicator* after it left the nest as long as it remained in the near vicinity. In Nyasaland, Wood has witnessed a similar fledgling greater honey-guide being mobbed by a number of birds—bulbuls (*Pycnonotus* and *Chlorocichla*), puff-backed shrikes (*Dryoscopus cubla*), and weavers (*Uraeginthus* and *Amadina*). The noteworthy point about these birds is that none of them is victimized by the honey-guide, a fact that makes it difficult to interpret the situation. This observation is the only one of its kind that has come to my attention, and I venture to suggest that the "mobbing" may have been begun by some species of fosterer, and that the other participants became excited by the action, joined in, and "took over" by the time the observer made his notes.

Flocking: The greater honey-guide is usually found singly, and prolonged observation of individual birds bears out their essentially solitary mode of living. Occasionally several are found together, especially when attracted to an opened bees' nest. Swynnerton (1908, p. 412) records seeing four of the birds at such a spot in Gazaland, and Chapin writes that a party of four is the largest number he had seen in the Belgian Congo. At Maktau, Kenya Colony, in May, I saw a loose flock of about seven or eight immature birds, in the yellow-throated plumage, in attendance on a few oryx antelopes, apparently catching insects scared up by the grazing beasts. Capt. Pitman writes me that he has also seen parties of up to half a dozen yellow-throated birds, never adults or mixed parties, and Serle (1939, p. 698) observed a similar group of young birds at Kafanchan, northern Nigeria.

Parasites: No species of *Mallophaga* have been described or recorded in print from any honey-guide, but Miss Theresa Clay informs me that in the collections of the British Museum there is a specimen of an undescribed species of the genus *Penenirmus* from *Indicator indicator*. The bird lice of the genus *Penenirmus* were previously known from Passeres, Picidae, and Capitonidae. Miss Clay states that the one taken from a greater honey-guide superficially resembles more some that are known from woodpeckers than it does those from barbets.

Thanks to the kind cooperation of Dr. W. Büttiker, formerly of Salisbury, Southern Rhodesia, and of Dr. Joel Warren and Maj.

Ray Cowley of the Department of Bacteriology, Army Medical Services Graduate Laboratories, Washington, D. C., something has been learned of the intestinal bacterial flora of this honey-guide. The following micro-organisms have been identified: *Aerobacter aerogenes*, *Pseudomonas antirubrum*, *Bacillus firmus*, *Escherichia intermedium*, an undetermined species of *Paracolobactrum*, one unidentified form of the *Bacillaceae* group, and one of the *Enterobacteraceae*. This list does not necessarily include all the intestinal organisms of the bird, but only such as were either viable or uncontaminated in the cultures by the time they were received in Washington. In general, they represent the common flora of the gastrointestinal tract of most mammals and birds.

ENEMIES: Andersson (1872, p. 224) states that this honey-guide sometimes falls a prey to the attacks of the bees, whose hives it seeks, when a number of the bees settle on or about its eyes. The birds' remarkably tough skin is often assumed to be a protection against bee stings, but, of course, the eyes are not protected by it. Pillain (1873, p. 215) also mentions that bees may attack the eyes of the birds, and cites as his source a statement by Le Maout (1843) to the effect that the dead body of a honey-guide was found in a bee tree, and that the bird had been killed (apparently) by the bees. I know of no recent statement or other observations supporting these older ones, and this would seem to argue for the relative infrequency of such occurrences.

No one has yet reported the greater honey-guide to be eaten by birds of prey or by carnivorous mammals or snakes, but the absence of definite records does not necessarily imply any immunity.

DESCRIPTION

ADULT MALE: Forehead and lores dark chaetura drab to fuscous black; crown, occiput, sides of face (except for auriculars), nape, interscapulars, upper back, and back chaetura drab to dark olive brown; greater, median and outer lesser upper wing-coverts also chaetura drab to dark olive brown, edged, but not tipped, with white, more broadly externally than internally, the inner lesser upper coverts broadly edged and tipped with bright primuline yellow, forming a broad diagonal band of this color; primaries and secondaries dark olive brown to chaetura drab, the secondaries externally and terminally edged narrowly with paler, more olivaceous brown; upper back and middle back dark olive brown to chaetura drab; feathers of the rump and upper tail-coverts dark olive brown to chaetura drab medially, broadly edged laterally with white, the width of the white margins increasing on the longest upper coverts to the extent that these feathers have only shaft streaks of brown; median pair of rectrices dark chaetura drab to dark olive brown, the next pair similar but with the inner web largely white, except terminally, the subsequent pairs with the white extending progressively over more and more of the outer web as well, but all of them broadly tipped with dark olive brown, these dusky terminal areas continuing basally along the outer edge of the outer web of each feather a short distance; auriculars grayish white; chin and throat like the lores but even darker, more blackish, sharply defined from the rest of the underparts which are white washed with pale drab gray, this wash usually strongest on the breast and upper abdomen, and weakest posteriorly; a few of the feathers of the flanks and thighs with dark olive brown narrow shaft streaks; under tail-coverts white; under wing-coverts similar but usually more heavily tinged with pale drab; bill pinkish white (varies in different individuals from strongly pinkish to grayish white to pale brown, the pink color disappearing from specimens after death; bill darker, more brownish in first adult plumaged birds, and (possibly) in birds in the nonbreeding season—this last still subject to further elucidation before it may be said to be definitely known); iris brown; tarsi and toes dark bluish green to dark plumbeous gray. Measurements in millimeters: wing 107–119, tail 67–78, culmen 13–15.5, tarsus 16–18. Weight, 58.8 grams.

Adult female: Similar to the adult male but with the general coloration of the top of the head and the upperparts generally somewhat paler—olive brown, sometimes with a buffy tinge; the forehead and lores even slightly paler, the chin and throat whitish tinged with drab, like the rest of the underparts; the pale edges of the greater, median, and outer lesser upper wing-coverts less whitish, more pale drab, the yellow edges of the inner lesser upper wing-coverts less bright, slightly darker as a rule; occasional very old females acquire some black feathers on the throat. Measurements in millimeters: wing 96–110, tail 54–68; culmen 11–13, tarsus 16–18.

Juvenal (sexes alike): Entire top and sides of head, nape, interscapulars, scapulars, upper wing-coverts, remiges, and back chaetura drab to dark olive brown with a wash of dark citrine to olive green, this tinge most pronounced on the forehead, crown, upper wing-coverts and on the edges of the median and greater upper wing-coverts and of the remiges, particularly of the secondaries; the remiges internally edged with whitish (hidden in closed wing); feathers of the rump and the upper tail-coverts white forming a conspicuous area of white (which is streaked with olive brown in the adults), although occasionally some of the feathers have some laterosubterminal blotches of brown; rectrices as in the adult but with the brown terminolateral patches on the outer rectrices usually somewhat smaller; chin, throat, and breast Naples yellow to pale mustard yellow; rest of underparts of body, under tail-coverts, and under wing-coverts white, somewhat tinged with pale grayish buffy; iris brown, eyelids grayish brown; bill blackish, often with a pinkish tip, tarsi and toes bluish gray, the undersurface of the toes sometimes pinkish. The remiges and rectrices in this plumage are somewhat narrower, more pointed terminally, than in the fully adult plumage.

The postjuvenal molt is incomplete, as it does not involve the remiges and rectrices.[29] This makes it possible to distinguish the first adult plumage from subsequent ones. Also, frequently, the chin and throat retain some of the yellow juvenal feathers in varying amounts. The first adult plumage is worn but a short time when the old, juvenal remiges and rectrices are replaced. The wing molt appears to antecede slightly the caudal ecdysis and seems to have but one center of origin, the carpal joint. The margins of the juvenal upper wing-coverts, scapulars, and interscapulars become extremely faded by the time the postjuvenal molt begins, being much tawnier, more sandy, less olivaceous than when fresh. The molt appears to begin rather irregularly in the scapulars and interscapulars, then starts on the chin and throat, and the upper wing-coverts and tail-coverts. The upper tail-coverts are all replaced and the new ones full grown before the upper wing-coverts are through molting. The last areas to molt are the forehead and crown. Verheyen (1953, pp. 117, 131) records that the rectrices are shed and replaced two pairs at a time, starting with the median two pairs. He finds that the wing molt begins during the egg-laying season.

This species is remarkably uniform throughout its vast range; no subspecies are recognizable. I have examined over 1,100 specimens from all parts of the range in the collections of the museums of Europe, America, and Africa.

Native Names

I have noted the following native names for this species recorded in scattered places in the literature. The list makes no pretense to completeness, and in all such compilations of transcriptions it should be kept in mind that there is always the possibility that the original recorders either may have misunderstood what the natives were telling them or may have misidentified the bird to which a particular name may apply. The names are listed alphabetically for ready reference.

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[29] Verheyen (1953, p. 123) states that in the postjuvenal molt the fourth and fifth pairs of primaries are replaced. I have seen no evidence of this.

Native name	*Tribe*	*Locality*
Chepkeche	Nandi	Kenya Colony
Harharit *or* H'arh a ret	Tigre	Ethiopia
Klavabizelwayo	Zulu	Natal
Johoroi	Masai	Kenya Colony
Kasolu	Lunda	Northern Rhodesia
Kaxibo	—	Angola
Kerkerié	Tigre	Ethiopia
Kihegu	Pangani	Tanganyika Territory
Kizigua	Segu	Tanganyika Territory
Marakaranga	Mashona	Southern Rhodesia
Maras *or* Maris	Somali, Tigre	Ethiopia
Mchamo *or* Mschlanvo	Kaffir	South Africa
Mlembo	Kikami	Tanganyika Territory
Moroc	—	Ethiopia
Msadzu	Nyanja	Northern Rhodesia
Mwana amuvanjee	Tonga	Northern Rhodesia
Ndege beia	—	Tanganyika Territory
Ndege ya Asali	Kiswahili	Tanganyika Territory
Ngede	Zulu	Natal
Nhalala	Tonga	Northern Rhodesia
Njolo	Lozi	Northern Rhodesia
Njuni	Bemba	Northern Rhodesia
Nomtschehetshe	Zulu	Natal
Nsedhlu	Ndebele, Sintabele	Southern Rhodesia and South Africa.
Nsola, *or* Nsole, *or* Nsolo	Bemba, Bisa, Nsenga, Nyanja, Tonga, Tumbuka.	Northern Rhodesia
Ntakobusi	Xhosa	South Africa
Ntlava	Zulu	Natal
Ntlavebizelayo	Zulu	Natal
Pala	Banda	French Equatorial Africa
Phetlo	Setho	South Africa
Pohoroi	Masai	Kenya Colony
Sazu	Sofala	Mozambique
Schneter	Shuma Arab	Northeastern Africa
Sequi	—	Angola
Solo	Tumbuka	Northern Rhodesia
Solwe	Tonga	Northern Rhodesia
Tetio	Mandingo	French Equatorial Africa
Tongoé	Wanyamwezi	Tanganyika Territory
Trogbo	Banda	French Equatorial Africa
Tschlo	Setho	South Africa
Tsese	Setho	South Africa
Tsewe	Sechuana	South Africa
Turubwa	Azande	Belgian Congo
Unomtsheketshe	Zulu	Natal

In addition to the above, the following names seem to be applied to honey-guides generally or, at least, to uncertainly identified species.

Native name	*Tribe*	*Locality*
Kasekwe	Chokwe	Northern Rhodesia
Mayimba	Lunda, Tonga	Northern Rhodesia
Mlembe	Kami	Northern Uluguru, Tanganyika Territory.
Moneschi nyuki	Kiswahili	Tanganyika Territory
Nsadzu	Ngoni, Nyanja, Tumbuka	Northern Rhodesia and Nyasaland.
Nsigu	Khonde	Nyasaland
Ntakobus	Zulu	Natal
Piegu	Zigua	Tanganyika Territory
Segu	Yao	Nyasaland
Shegu	Bondei, Pangani, Zigua	Tanganyika Territory

Malayan Honey-Guide

Indicator archipelagicus Temminck [30]

FIGURE 1; PLATE 21

Very little is known of the habits of this honey-guide, and nothing at all regarding the points of greatest interest—whether it guides to bees' nests and whether it is parasitic in its breeding habits. Judging by the wide occurrence of parasitism throughout the family, one might expect this species to be parasitic also, but there are no observational data.

DISTRIBUTION

The Malayan honey-guide is known from only a small number of records from localities in southern Siam (Chong, Trong, Peninsular Siam, and Klung River, Khlong Khlung District); the Malay Peninsula (Klang, Selangor; Ginting Bidai on the Selangor-Pahang boundary; Gunong Tahan; Kuala Taku at foot of Gunong Tahan, Malacca), Sumatra (Basilan, Lesten, Panobasan, Langkat), and Borneo (Pontianak; Kuching; Saribas District; Karou River; Poelau; Lumbidan, northwestern Borneo; Kapuas River; Benkoka, northern Borneo; Mengalung River, northern Borneo; Paun, Tebekang area; Satang Island, off mouth of Sarawak River, Mount Dulit, 2,000 ft.; Bintulu; near Samarahan Estate and Trusan, Sarawak). Specimens have been taken from about sea level (100 feet above at Paun) to at least 3,000 feet above sea level (Gunong Tahan, Malay Peninsula). As may be seen from these records, this honey-guide has been met with chiefly in the Malay Peninsula and Borneo; there are only two records from Siam and four from Sumatra. It has not been reported from Java.

The species is said to be a forest dweller, and, being a bird of the tree-tops without bright coloration or loud vocalisms, it may possibly be overlooked to some degree, and may not be quite as rare as the paucity of records would indicate. Recently, Hoogerwerf (Chasen and Hoogerwerf, 1941, p. 42) obtained a specimen from a low shrub in pasture land near Lesten, northern Sumatra. This suggests a wider habitat range than a purely sylvan one, and this, in turn, together with the fact that there is a Malay name for it, "musoh lébah," at least suggests that the bird may be common enough to be known to some of the people (if the name is really restricted to the one kind of bird, and not a general name for any smallish species).

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[30] *Indicator archipelagicus* Temminck, *in* Temminck and Laugier de Chartrouse, Nouveau recueil de planches coloriées d'oiseaux . . . , livr. 91, pl. 542, fig. 1, 1832. (Pontianak, Borneo.)

Harrisson informs me that on April 1, 1953, he saw a honey-guide on Satang Island, which is about 10 miles off the mouth of the Sarawak River. The point of this record is that he doubts that the bird is strictly resident on a small island, and suggests that the species may be something of a wanderer. Satang Island has a very limited bird fauna.

The only indication of a breeding date is that suggested by an adult male with considerably enlarged gonads that was taken at Paun, southwestern Sarawak, February 14, 1950. There is no reason to think that this honey-guide is other than resident wherever found, but it is not impossible that it may be subject to slight movements due to seasonal factors such as the flowering of the *Dipterocarpus* trees, and the resulting influence on the abundance and activity of wild bees. We have, however, no information

ASSOCIATION WITH BEES

Guiding is not known to occur, but so very few people have ever even seen this species alive that this does not necessarily mean anything. Chasen (1939, p. 166) admits complete lack of knowledge, but notes that in Malaya the bird has been met with only at places and times at which bees were unusually numerous. Two specimens were shot from trees "near water when tall *Dipterocarpus* trees in flower were attracting swarms of bees." Of two other examples from the Malay Peninsula, Robinson and Kloss (1911, pp. 44–45) note that one was shot in the vicinity of a bees' nest and both were taken in deep forest by native assistants. One collected in Sumatra by Jacobson (in Robinson, 1928, p. 97) was perched in a very high tree. Lowe (1933, pp. 476–477) writes of it in Siam that it is a very retiring bird, easily overlooked among the dense foliage of the trees. There appear to be no recorded native legends about this bird that connect it with bees' nests or with any guiding behavior. In Borneo, according to Hose (1912, p. 154) the natives get honey and beeswax from the wild bees' nests which are suspended from high branches of the trees; sometimes there are many nests in one tree. The taking of the contents of these nests is usually accomplished after nightfall. The fact that the natives open the bees' nests after dark suggests that no cooperation by *Indicator archipelagicus* is involved, as it is quite unlikely that this bird is active at night (at least, as far as one may judge from its African relatives). Harrisson (in litt.) writes me that he does not think there is any probability of its guiding humans to bees' nests.

Songs and Calls

The calls of this honey-guide are described by Harrisson (1950, p. 334) in Sarawak as follows. "We first heard a noise almost exactly like a domestic cat's '*miaw*,' but coming from a 150 foot tree. This was repeated with deep notes and an appendix which I recorded as best I could on the spot as '*miaw-krrruuu*.' It was hard to see the bird, which looked indistinctly like a bulbul . . . Shot for identification, it proved to be yet a fourth male, gonads considerably enlarged." The suggestion of a purring quality in the ending of this rendition reminds one somewhat of the "song" of the male scaly-throated honey-guide. A variation of this utterance is described in Sumatra by Jacobson (in Robinson, 1928, p. 97), who found a bird perched high in a tall tree, uttering incessantly its note, which consisted of the sound *è* repeated several times, followed by a whizzing *rrrr*.

Food

Knowledge of the food of the Malayan honey-guide rests on the reported contents of the gizzards of two individuals collected. One, taken near Paun, Tebekang area, Sarawak, contained parts of the fresh comb of a beehive as well as whole bees and bee larvae (Harrisson, 1950); the other, shot on the Khlong Khlung River, Siam, contained beeswax. Thus, there is an essential similarity here between this species and its better known African congeners.

Recently Harrisson (in litt, April 1953) watched one of these birds pecking at some largish insects on a branch of a tree about 20 feet from the ground. There were many flowers just below the tree and the insects might have been bees. The bird moved in a rather heavy, almost squirrellike way along the branch while feeding.

Description

Adult male: Upperparts of head, body, and wings olive brown to dark olive; the feathers of the back and wings edged with ecru olive to light yellowish olive; primaries, secondaries, and greater upper wing-coverts with pale buffy brownish inner margins, the inner lesser upper wing-coverts bright lemon chrome; feathers of lower back, rump, and the upper tail-coverts with the edges pale light yellowish olive to almost white, producing a sparsely streaked appearance; rectrices dark olive brown, partly edged with ecru olive, paler at the base, the three outer pairs partly dusky whitish on their inner webs, the three median pairs with narrow pale buffy brown to buffy whitish edgings on their inner webs only; sides of head dingy drab grayish white with a faint olive tinge, the auriculars similar but darker, hair brown to dark grayish olive; chin whitish, throat and breast similar but washed with olive grayish to ashy buff; rest of underparts dirty white, tinged with grayish buff on the abdomen and under tail-coverts; feathers of flanks and thighs with broad shaft stripes of dull blackish brown; under wing-coverts creamy white with brownish shafts; iris crimson (also described as Indian red and as bright scarlet), bill dark horn brown, duskier terminally (also described as dark gray on the maxilla, pale gray on the mandible); tarsi and toes variously described as dark gray, blue, or leaden green, with slate claws. Measurements in millimeters: wing 91.5–101.6, tail 65.5–71, culmen, from base, 14–14.8, tarsus 14–14.3.[31]

Adult female: Similar to the male, but without the yellow band on the lesser upper wing-coverts, and somewhat smaller in size. Measurements in millimeters: wing 86.4–89, tail 56.5–66, culmen from base 11.8, tarsus 12.7.

Juvenal: "Similar to the adult, but differs in having the upper parts slightly more washed with yellow, with a mere trace of the yellow shoulder-spot; tail identical in colour; throat faintly striped; lower throat and chest less ashy and slightly washed with yellow." (Shelley, *in* Catalogue of the birds in the British Museum, vol.19, p. 4, 1891; based on Sharpe's description of *I. malayanus*, now considered to be a young *I. archipelagicus*. In view of the fact that the adult female lacks the yellow shoulder patch, it would seem that Sharpe's bird, which was unsexed, was probably a young male.)

Natal down: Unknown, if any; color of skin and soft parts unknown.

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[31] Chasen (1941, p. 42) gives wing measurements of five males from Borneo as 89–94 mm., of two from Sumatra as 98–100 mm., and two from the Malay Peninsula as 98–102 mm., of two females from Borneo as 84–91 mm., one from Sumatra as 86 mm., and three from Malay Peninsula as 85–89 mm. He notes that a male from Pahang, Malay Peninsula, differs from Bornean and Sumatran males in its more robust bill and slightly grayer, less olive crown. The Sumatran male has grayish streaks on its throat, but all the differences are slight.

Lesser Honey-Guide

Indicator minor Stephens [32]

FIGURES 1, 2,*d*, 3,*f*;
PLATES 3, 4, 5, 6,D,E, 7, 10, 11, 14, 16, 17, 23

DISTRIBUTION

ECOLOGICAL RANGE: The lesser honey-guide is a wide-ranging bird inhabiting (taking all its races together) almost every conceivable habitat from evergreen tropical forest to arid, sparsely wooded areas such as parts of Somaliland and of Damaraland. Some of the subspecies are in themselves very restricted ecologically—*conirostris*, for example, being entirely a denizen of the dense, evergreen tropical forest, and *damarensis* living only in the dry steppes of the highlands of Damaraland—while others, such as the nominate race, are found in a greater variety of habitats. Thus, in Kenya Colony alone, *minor* is known to inhabit riverine or gallery forest (South Kinangop, Aberdare Mountains, at 8,000 feet), the dry highlands forest, dry bush country, savannas, and the very dry thorn-bush areas. Its altitudinal range extends from sea level up to at least 8,000 feet. In Nyasaland, Benson (1953, p. 45) records it as occurring below 5,000 feet in rainforest or in any type of woodland.

GEOGRAPHICAL RANGE: Africa south of the Sahara from Senegal on the west to Eritrea and Ethiopia on the east, south to the Cape Province. In this enormous expanse the species breaks up into a number of races, whose distribution may be given separately.

I. m. senegalensis. [33] Senegal (Thiés, near Dakar).

I. m. alexanderi: [34] French Sudan (Mopti), the northern territories of the Gold Coast (Kintampo, Gambaga, Bole), northern Nigeria (Bauche and Benue Provinces, Nasaru, Ilorin), Lake Chad (Fort Lamy), east probably to the Shari and Bagirmi areas; in open, sparsely wooded savannas, not in dense, evergreen forest.

I. m. ussheri: [35] Liberia (Firestone Plantation) to the Ashanti area of the Gold Coast (Ejura, Mampong). [36]

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[32] *Indicator minor* Stephens, *in* Shaw, General zoology, vol. 9, pt. 1, p. 140, 1815. (Cape of Good Hope=Zwartkop River, Uitenhage Division, Cape Province.)

[33] *Indicator minor senegalensis* Neumann, Bull. Brit. Ornith. Club, vol. 21, p. 43, 1908. (Thiés, near Dakar, Senegal.)

[34] *Indicator minor alexanderi* C. Grant, Bull. Brit. Ornith. Club, vol. 35, p. 99, 1915. (Gambaga, Gold Coast Hinterland.)

[35] *Indicator ussheri* Sharpe, Bull. Brit. Ornith. Club, vol. 12, p. 80, 1902. (Fanti, Gold Coast.)

[36] As long ago as 1828, Lesson (1828, p. 125) reported the lesser honey-guide from Sierra Leone. No one has found it there since, but if this is to be taken as a valid record, it might well refer to this race. It is not sufficient evidence, however, on which to extend the known range of this form that far westward.

I. m. pallidus:[37] The greater part of Nigeria, except parts of the northern areas; confined to high forest or to broken forest at the edge of the dense forest (Umuagwu, Owerri Division; Kanno, Plateau Province, and between Ilesha and Erinomo, Western Provinces).

I. m. conirostris:[38] The dense evergreen forests from southern Cameroons (including Mount Cameroon; Bitye, Doum, Sangamelima, River Ja, etc.), Spanish Guinea (Bebai) and Gaboon (Moonda River, Oyem), eastwards across the Belgian Congo (where it inhabits mountain forests on Ruwenzori (6,800 feet) as well as lowland forests; Kamituga, Koteli, Ibembo, Wago-woud, Buta, Lukolela, Beni, Nganji-woud, Kalongi) east to Mount Elgon and to Kakamega and Kapenguria, western Suk area, in western Kenya Colony.

I. m. riggenbachi.[39] Northern Cameroons (Tibati and Dodo, Adamaua) and the Shari basin to Darfur and the Bahr-el-Ghazal area in the Sudan (Bongo, Shambi), south in the Belgian Congo to the northern Uelle and Lado districts, and along the eastern edge of the Ituri forest south to the base of Ruwenzori (Aba, Ukondju (north of Lake Edward), Mahagi Port, Ischwa, Meberg, Tobbo, Karevia, Butahu valley, Beni). It is not yet clear just where, in the Shari area, this race meets *I. m. alexanderi*, or where, in the Sudan, it merges with *I. m. diadematus.*

I. m. diadematus:[40] Southeastern Sudan (Sennar, Mongalla, and Upper Nile Provinces; Roseires, Kenisia, Shamba, near Lake No, Dinder River, Torit, Kamisa) to Ethiopia (El Dire, Tertale, Yavello, near Arero, Gelongol, Darror River, Djamdjam, Galana River, Daroli River, Gerwidja) and Eritrea (Assaorta, Anseba, Debrimela, Miniferi, Waliko (Bogosland)) to British Somaliland, and northern Italian Somaliland (Waghar, Wagga Mountain).

I. m. minor: Northern Angola (Quibula, near Benguella, south to Gambos where one specimen may be intermediate towards *I. m. damarensis*), Belgian Congo (south of the great forest—Manyema, Kabubu River near Elisabethville, Katanga, and Moba and Lake Suse in Marungu; and east of the forest north to Kabalo, Kasaji on the Lualaba, and to the Luvua River at the eastern base of the Ruwenzori Mountains), Uganda (Toro, Kampala, Kitgum, etc.), Kenya Colony (throughout), southern Ethiopia (Gato River near

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[37] *Indicator conirostris pallidus* Marchant, Bull. Brit. Ornith. Club, vol. 70, p. 25, 1950. (Umuagwu, Owerri Division, Southern Nigeria, twelve miles southwest of Owerri on the road to Port Harcourt, lat. 5°20′ N., long. 6°55′ E.)

[38] *Melignothes conirostris* Cassin, Proc. Acad. Nat. Sci. Philadelphia, vol. 8, p. 156, 1856. (Moonda River, Gaboon.)

[39] *Indicator minor riggenbachi* Zedlitz, Journ. Ornith., vol. 63, p. 12, 1915. (Tibati, Adamawa highlands.)

[40] *Indicator diadematus* Rüppell, Neue Wirbelthiere . . . , p. 61, 1837. (Forested parts of Ethiopia.)

Gardulla, Mfudu, Helleschid) and southern Somaliland (Afgoi, Serenli, Unsi, and Jubaland) south throughout suitable areas in Tanganyika Territory, Mozambique, Nyasaland, the Rhodesias, and Bechuanaland to the Cape Province, except for the highlands of Damaraland; in South Africa absent from the dry western treeless areas.

I. m. damarensis:[41] Damaraland (Quickborn, Otjosongomba, Ukuib, Rietfontein).

Breeding Range and Season

The lesser honey-guide has been found breeding in the following places and at the times indicated. However, the data are very meager and incomplete for many parts of Africa, and, consequently, the data here recorded may be extended considerably when new information is available.

South Africa: Many records. Eggs from September 27 to February 27, but the bulk of the records being in October, November, and December. Eastern Cape Province, from October 17, 27, to December 7; Natal, September 27 (Umsonga), "late October," November 17, December 4, 12, and February 2; Zululand, October 20, November 12, December 1; Transvaal, October 20, 29, December 6, 10, 11, 17.

Southern Rhodesia: Eggs, Strathmore, October 10 to November 19; Marandellas, October 10, 20, November; Matopos Research Station, October 30; Plumtree, October 21; fledgling, Wedza, November 15.

Northern Rhodesia: Egg date, Lake Mweru, October 13; specimens with large gonads, Kafue River, late December.

Nyasaland: Egg, October 13; eggs attributed to this species in September, October, November.

Tanganyika Territory: Ngare Nairobi, near Kilimanjaro, March 3, two females collected in breeding condition; Karogwe, November 12, one male collected with testes about half breeding size; also breeding birds September 10; breeds in December (Mackworth-Praed and Grant, 1952, p. 743).

Kenya Colony: Nairobi (Ngong area), nestlings April, May, June, and August; coastal belt, nestlings May and June; Teita Hills, one female collected with somewhat enlarged ovary November 6; Meru near Mount Kenya, July 25, male with slightly enlarged testes; Kibwezi, female with well developed ova, March 17.

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[41] *Melignothes minor damarensis* Roberts, Ann. Transvaal Mus., vol. 12, p. 308, 1928. (Quickborn, Southwest Africa.)

Uganda: Adult females in breeding condition reported (without locality) between March 17 and July 5.

Anglo-Egyptian Sudan: Kidepo River, 50 miles east of Torit, female with greatly enlarged ovary, April 24.

Ethiopia: "Said to be breeding" in April.

Belgian Congo: Lukolela, female with soft egg in oviduct, December 12; Mahagi Port, egg, May 18; southeastern Belgian Congo, breeds in October according to Mackworth-Praed and Grant (1952, p. 743); Upemba Park, birds with enlarged gonads, March 18 and June 3.

Cameroons: Bitye, egg, late October; nestling, April 1.

Nigeria: Owerri, females in breeding condition collected May 11, August 3, and October 24; seen around colonies of *Gymnobucco calvus* in all months but June.

Gold Coast: Ejura and Mampong, males collected with testes beginning to enlarge February 8, 11, suggesting breeding a few weeks later.

Liberia: About 35 miles from Monrovia, female with large ovarian egg, September 30.

Songs and Calls

The "song," or, as it has been called, the "song-call" is a one-toned, unmodified, repetitive, monotonous, faintly throaty *kleeu* or *peew* note given in series of from 10 to 30 notes. The note is not loud even when heard at close range, but, when once known, can be heard and recognized at least 200 yards away. The interval between series is from half a minute to two or even three minutes, usually nearer the shorter than the longer time, and there is no appreciable variation in pitch, tempo, or intensity, no alteration in scale, and no difference between notes except for the fact that the first note of a series is often drawn out almost into two syllables, *klee-eu* or *pe-ew*. I have heard it dozens of times and have never heard it except from a bird perched in a call-site tree. A person not familiar with the sound would easily pass it by unheard, and would probably conclude that the lesser honey-guide is a very silent bird. As the bird is apt to sit in a sheltered place under the canopy of the foliage of a tall tree, and as it blends in color with the olive shadows of the leaves, it is quite inconspicuous and is undoubtedly overlooked by many naturalists. Were its vocalisms more conspicuous and commanding of attention the bird would be recorded much more frequently.

It is not definitely known if this song-call is given only by the male, or if the female may also "sing." According to information from Pringle and Ranger, two birds collected after having been heard singing from a call site day after day turned out to be males. Judging solely by analogy with the greater honey-guide, it seems probable that any bird singing constantly from a definite tree will prove to be a male. But, it must be emphasized, this is not proved, as analogy is by no means a conclusive argument.

If the *kleeu* note is given only by the male, it would appear that, as far as recorded information goes, the female lesser honey-guide is wholly silent. I doubt that this is really the case, however.

When feeding, the birds do not call; at least I never heard any sound from them as they darted about after flying insects. Skead (1951, pp. 52–53) noted that even when two of the birds were together in his garden and one chased the other energetically, they remained silent. On two occasions only did he record any call notes—a quiet, unaccented, stuttering trill which he rendered as *tttrrreee.*

In Cameroons, Bates noted a little chirping call from the local race, *I. minor conirostris*, but found it usually to be silent. In the Belgian Congo, Chapin apparently heard no notes from either *conirostris* or *riggenbachi,* as he describes none in his accounts. Similarly, in Nigeria, Marchant (1951, p. 73) never heard *conirostris* utter a sound.

The *kleeu* notes are given from about an hour or so after sunrise, about 7:30 a. m., to about two hours before dusk, about 4 p. m. It is my experience that on cloudy or rainy days the song is given as much as on sunny days but the number of notes in the series tends to be smaller, about 7–15, as compared with up to 30 on sunny, bright days.

The call note of the nestling is described by Skead (loc. cit.) as a "rolling, squeaky noise heard continuously throughout the day and even into the night . . . It closely resembles the call of the chicks of its host, the Black-collared Barbet, and also the chick of the Greater Honeyguide. As the chick gets older the calling becomes less persistent."

Seasonal Movements and Site Tenacity

As in the greater honey-guide, there is no true migratory movement in this species, but some local, seasonal moving about is indicated by the following observations.

Heuglin (1869, pp. 771–773) considered it a migratory bird in northeastern Africa, arriving singly or in "pairs" in Samhar, Ethiopia, and in the drainage basin of the White Nile (subspecies *diadematus*). In the West Basin of the Darfur Province, Sudan, Lynes (1925, p. 352) never met with the species (subspecies *riggenbachi*) except for a visitation during July and August, when it suddenly appeared in some numbers. "These midsummer visitors were fairly plentiful in the woodlands; all our specimens [seven collected] were adults in well-advanced complete moult; five of them came from one party. I think they must have come from somewhere to southward of Kulme, having bred there . . . about April."

In eastern Cape Province, Pringle (in litt.) has seen the lesser honey-guide "during the winter, but not as many as during summer, so I am sure the majority move off." However, throughout most of its range, and especially in the northern and southern peripheral portions of it, where, if anywhere, one might expect evidence of migration, the species has been recorded definitely throughout the year. It cannot be called migratory in a true sense.

In the Umtaleni Valley, near Kei Road, eastern Cape Province, Ranger trapped and banded a lesser honey-guide on March 3, 1953. The bird was taken by C. J. Skead the same day to King William's Town, roughly 15 miles away, and there released. Some eight months latter, on November 26, it was recaptured in the Umtaleni Valley. The distance involved, while not great, is much greater than an individual bird would be expected to wander "normally" in its feeding range. The fact that the bird was not recaptured until more than eight months later does not necessarily mean anything, as it might have come directly back from King William's Town in a day or two and remained unobserved until its recapture. The same individual was captured again on June 22, 1954, and taken to East London where it was released three miles from the coast. On November 14 it was retaken at Umtaleni. The distance involved was 27 miles in a straight line.

As is shown in our discussion of the call sites of the adult males, it appears that the same individuals may be found day after day, for months on end, calling from certain spots. This does suggest site tenacity of a sort, but as yet in most cases we have no proof that the bird in any one call spot is always the same individual. However, in one instance we do know this to be the case; a bird ringed and color-marked by Ranger "took over" a favorite site the day after a singing male was shot there (to ascertain the sex of the calling bird). This individual, easily recognizable, remained at the call site throughout that season (1952–1953) and returned there again the following summer (October, 1953). It seems that this case is a perfectly normal one and reflects the usual situation, but aside from it we have only a rather contradictory group of loose observations and statements. Thus, for example, Skead (1951, p. 56) never saw anything "to indicate any territorial instinct in the adult honeyguide. Indeed, because of their uncommonness, it would appear almost impossible to solve this question. I believe the birds have an extensive range, and they are so scarce that the possibility of clashing with others of their kind is remote."

On the other hand, Pitman writes me from Uganda that he has the impression that these birds establish very definite territories, although he qualifies this statement by admitting that he has no supporting evidence for it. In answer to a query of mine, Pringle (in litt.) writes that on his large farm at Bedford the honey-guides (both *I. indicator* and *I. minor*) have definite localities of large area and that he has never observed any fighting for possession by the birds. Inasmuch as Pringle's observations were summarized from memory in his communication, I cannot help but wonder if the large area of the supposed "territories" may not mean merely that the distance between call sites was very considerable.

More information is highly desirable.

Courtship and Mating

There is almost nothing in the literature on the courtship and mating habits of the lesser honey-guide except for one little note on the Nigerian race, *alexanderi*. Brown (1948, p. 535) observed "individuals of this species performing a curious flight, perhaps a form of display. The bird flies round in circles at great speed. Two violent wing-beats are followed by a short glide, so that the flight is markedly undulating. The wing-beats occur at intervals of about half a second, and are accompanied by a loud clapping sound, as if the wings were being struck together. The whole sound-effect is like a motor bicycle firing irregularly."

This rustling flight has also been observed in the nominate subspecies in South Africa. Near Kei Road, eastern Cape Province, Ranger informed me that he has seen *Indicator minor* fly around several times in a circle about forty yards in diameter, constantly dipping as it flies, and with each dip making a whirring noise with its wings—a single whirring, not a double one as in *Indicator indicator*. Whether this rustling flight is a courtship performance is not clear, and, without further evidence, we have no real way of interpreting it. Other observations of this behavior have come to me from Bedford, not far from Kei Road, and from near Uitenhage, farther to the west in the Cape Province. Mr. Darrel C. H. Plowes informed me that at Bedford on May 18, 1948, he and Victor Pringle watched a lesser honey-guide as it flew in short fast bursts with its tail spread, making a humming noise as it circled around them several times. After going around a few times it lit in a thorn tree where it began to give its song-call. Plowes had the impression that the resulting or humming sound was caused by the wind vibrating the tail feathers, but he could not be certain. The fact that the bird later began to "sing" suggests that it was a male, as the female is not known to give the *kleeu* note (but may yet be found to do so).

What seems to be a description of a "sexual flight" comes to me from Captain Pitman, who writes that one evening just before dusk at Mbarara, Ankole, Uganda, he saw two lesser honey-guides "following each other from tree-top to tree-top with a curious, dipping flight. All the time a persistent *pee-uw, pee-uw, pee-uw* was being uttered. I do not know if it was a pair, but I think I am correct in saying that only one of the birds was calling."

I have never seen any attempt at any posturing that suggested courtship antics, although I have watched male birds for hours at a time. In this my experience is corroborated and amplified by that of Ranger, Skead, and Pringle in the Cape Province and by other observers in other parts of Africa. Skead (1951, p. 53) writes that he has seen no displays whatever, the general disposition of the birds being one of lazy indifference. Two birds, not proved or even stated to be a pair, although written of as though they might have been, stayed together in Skead's garden from July to September, and were "for the most part, amiable but sometimes one for no apparent reason would attack the other (perhaps sitting in another tree) and chase it up and down the garden two or three times until the chased bird, closely followed, dived into a shrub where the two would sit panting heavily. Either the display would then cease or the aggressor would attack again. All this was done in silence."

A peculiar bit of behavior, possibly connected with what would pass for courtship in other birds, is the following account related to me by J. G. Williams of the Coryndon Museum. Near Thika, Kenya Colony, in July, he came across a remarkable concentration of lesser honey-guides, at least a dozen of the birds in a single large tree. They were perching on the branches, or settling momentarily, after the fashion of a tit, on the trunk itself. There was no bees' nest or other food supply in the tree.

> The birds, which were completely silent throughout, would constantly change their perches, and as they alighted would fan their tail feathers, showing the white outer retrices, and would continue to do this three or four times. Sometimes two birds would settle close together—an inch or so apart—when the tail fanning of both would continue much longer. Frequently a bird would leave its perch and settle on the bare tree trunk, its tail pressed against and fanned on the bark; sometimes they would alight on the trunk with their heads pointing towards the ground.

After watching the birds for an hour or so Williams shot one of them and found it to be a female with an enlarged ovary, perhaps within two or three weeks of breeding. At the shot the other birds flew off and did not return.

Obviously, it is not yet possible to fit these data into a definite place in the life history of the lesser honey-guide, but the increased duration of tail fanning when two birds were very close together, actually almost in contact, is suggestive that this action may be not foreign to courtship behavior. It may be recalled, in this connection, that the pattern of the white outer tail feathers, contrasting with the dusky drab olive median ones and the drab color of the entire body and wings, is the only striking color pattern in the bird's plumage, and, further, it may be recalled that the activities involved in courtship display, as generally found in birds, are frequently connected with revealing any such bold markings. We have here a clue, but only a clue. It suggests also the possibility of a mutual type of display, weak as it may be, since it appears that in those instances where two birds were close together both indulged in tail fanning. Further observations are greatly to be desired. Lest it seem too tempting to interpret these data as intersexual behavior, it may be well to recall that A. Roberts (1911, pp. 73–74) collected what he took to be a pair perched close to each other on the same branch of a tree near Boror, Mozambique, and found, on autopsy, that both birds were males.

As in the greater honey-guide, in this species we find that males resort to certain trees with great regularity and adhere to them most of the day and there give their monotonous, repetitive "song." Ranger (1932), in a short note in a local South African journal, was the first to record this for *I. minor*, as well as for *I. indicator* and *I. variegatus*. He merely noted that all three species have the habit of calling from a certain fixed spot for months on end, and that the greater and the lesser honey-guides both choose a tree on a hillside for the purpose. The Moreaus (1937, p. 173) noticed the same thing for *I. minor* near Amani, Tanganyika Territory. Their experience lead them to write as follows:

> One of these small Honey-guides will perch perhaps a hundred feet above the ground, and hour after hour, day after day, and month after month, reiterate its . . . monotonous song-call . . . . For the last five years we have recorded a noise which begins between May and August and continues throughout the hours of daylight until the following February. The constancy of position all this time has been amazing, and only this season has a rival established itself within earshot, about 300 yards away along the same forest edge.

At Dowa, Nyasaland, Benson (1940, pp. 429–430) heard *I. minor* daily, from May to October, calling from a big leafy fig tree in his garden. The bird "would call right through the heat of the day, though . . . never . . . until about an hour and a half after sunrise, and it would cease about the same period before sunset." This was, apparently, a similar call-site situation, even though its full significance was not specifically mentioned.

In the Umtaleni Valley near Kei Road, Cape Province, in November 1950, Ranger, Skead, and I observed the same situation—lesser honey-guides calling day after day from definite trees. Whereas the

Moreaus recorded one such call-tree in use for five years, Ranger's observations show that at Umtaleni individual calling posts have been in constant use for several times that long. Because of the paucity of recorded data, it may be well to report our observations in some detail.

There were two call posts in the Umtaleni Valley, one of which Ranger had known to be used ever since 1935—at least 15 years. The two were about 800 yards apart, but the second one was not used as constantly as the first. Actually, the first one was not a single tree but two favorite trees close together and two less-favored ones nearby. They were on a hillside thickly sprinkled with thorn trees. One of them was a cabbagewood tree; the others were thorn trees. About 150 yards downhill there was a stream bordered by a little wooded kloof, and occasionally the honey-guide would fly from its chief call site to this kloof where it would perch on one of the taller trees and give its song-call for perhaps 10 or more minutes and then fly back to its hillside station.

It was chiefly over the stream in this wooded kloof that it fed late every afternoon, hawking about for insects like a flycatcher. Like the greater honey-guide, it remained on its favorite call site from about 7:30 or 8 a. m. to about 4 p. m. Before and after these hours it was off feeding, chiefly in the kloof, but did not sing except from the call sites (either the favorite, hillside group of trees or those in the kloof). During the hours at the call site the bird not infrequently would fly out and catch an insect in the air and then return to its perch, combining feeding with singing at the call site much more than ever was observed in *Indicator indicator*.

An observation blind was constructed near the most favored of the trees comprising the call site, and from this I was able to watch a lesser honey-guide (presumably the same individual) at close range (10–15 feet) for hours at a time on several consecutive days. The bird was not seen or heard before 7:20–7:40 a. m. and was definitely gone after 4 p. m. During the hours of close observation the bird usually sat in a rather erect position under the foliage, where it was neither completely hidden nor wholly exposed, and "sang" a series of slightly throaty, somewhat plaintive *kleuu* notes, varying from 15–30 notes in a series. There was only a short space of two or three minutes between each series. The bird jerked a little when giving each of its notes, a slight quivering of the whole body and tail being noticeable at close range. There was no modification in accent, pitch, or intensity of the notes in a series, the result being a truly monotonous vocal performance.

To take a few typical observations, I extract the following from my field notebook.

> November 6. This morning I spent three hours in the blind at *I. minor's* favorite call spot. Heard and saw the bird as I approached at 8:05 a. m.; it flew downhill to the kloof as I came near but at 8:25 I heard it nearby again (could not see it from the blind). Soon it flew over to its usual perch where it was in plain view, and from then until 11:05 it gave a series of 15 to 30 *kleuu* notes every few minutes, but it never came down to a piece of honeycomb I had placed close to the blind the day before.
>
> November 10. *I. minor* first heard at 7:56 a. m. At 8:25 I went to the hillside call site where I found it calling from the cabbagewood tree. It flew off at 8:30 to the thorn tree near the blind, called one series of notes on arrival there, and then flew back to the cabbagewood tree and called from there, with intervals of not more than one minute between series, until I left at 9:30. The series of notes were shorter today, only 10–17 notes . . . At 10:40 I returned; the bird was still perched in the cabbagewood tree calling as before. It was almost concealed from below by the foliage, and as I stood directly beneath it I "squeaked" several times. which caused it to flit down from one perch to another until it was on the lowest branch only 15 feet from me, looking at me and jerking about from one position to another. It flew to another cabbagewood tree nearby, and kept looking in my direction, then back to the first tree. I stopped squeaking and it went off to the thorn tree near the blind. I then began squeaking loudly but it remained and kept calling in the hilltop thorn tree . . . At 11:20 it went back to the first cabbagewood tree and called from there every 60 seconds until I left at 12:05.

Judging by analogy with *Indicator indicator* it seemed that the bird calling so steadfastly day after day from the call site was probably a male but, inasmuch as the sexes of *I. minor* cannot be distinguished in the field, this point cannot be proved. However, Pringle told me that once at Bedford he shot a lesser honey-guide that had been giving a series of *kleuu* notes from a definite tree for some time and found it was a male. On his farm near Bedford, Pringle estimated that the known call sites of different individual lesser honey-guides are 1 to 1½ miles apart. At Umtaleni, Ranger and Skead in November 1952 shot a calling bird from a well established call site and found it to be a male. The next day there was another individual (presumably a male) calling from the same favorite branch of the tree. Thus, there seems to be a definite tendency for continuity of occupancy of such favored call sites.

In no case during our joint intensive observations in the Umtaleni Valley did either Ranger, Skead, or I ever see a second lesser honey-guide come to the call site, as we did in the case of the greater honey-guide. However, a year after my departure, Ranger and Skead were back at the same spot and trapped three lesser honey-guides alive. One of them conveniently layed an egg in the cage, thereby identifying itself as a female. This bird was marked and then released just below a calling male (?) at the favorite call site. The latter immediately dropped down to the released bird in what seemed a nonaggressive, rather gentle fashion, and the two flew away together. Almost immediately they returned together with a third individual. Where this last bird joined them is not known, but by trapping in the immediate vicinity of the call site Ranger and Skead found that at least six lesser honey-guides frequented the spot.

Inasmuch as nothing is known of the mating behavior of this species it is not possible to say if it is promiscuous like *I. indicator*. There are a few recorded observations that suggest that two individuals remain together for some periods of time, but these are not explicit enough to allow for an interpretation.

Skead (1951, p. 53) writes of two birds "keeping company" from July to September. In Abyssinia, Lovat (in Ogilvie-Grant, 1900, pp. 306–307) noted that in April lesser honey-guides were in breeding condition "and a pair flitted all around our camp most of the day." Beven (1945, p. 12) noted a "pair" in Zululand. In Mozambique, Donald Lamm writes me that on November 11 at Movene he saw a "pair, sticking close together, and hotly pursued by a black-collared barbet . . . which chased them from tree to tree chattering at them all the time. Usually they moved off when attacked, but never went far." As noted above in a different connection, A. Roberts (1911, pp. 73–74) collected a "pair" at Boror, Mozambique, which turned out to be two males. He considered this to be "remarkable, because they are very pugnacious and jealous of other members of their own species straying into their own particular hunting grounds." I know of no data bearing on any such implied territoriality or "jealousy," and I cannot help but wonder if Roberts may not have written beyond the evidence.

Eggs and Egg Laying

The eggs of the lesser honey-guide are pure white with a considerable gloss, oval in shape, and vary in size from 20.3–22.6 by 14.5–17.9 mm. (One egg, possibly a "runt" or a misidentified specimen, is said to measure only 10 mm. in width although 21 mm. long.) An egg taken from the oviduct of a bird collected at Mahagi Port, Belgian Congo, measured 21.5 by 16.8 mm., and may be looked upon as an absolutely authentic "reference" specimen (subspecies *I. minor riggenbachi*). Another, laid in a cage by a trapped bird (*I. minor minor*) in the eastern Cape Province, measured 22.5 by 17.0 mm. Ivy (1901, pp. 21–22) and A. Roberts (1913, p. 21) each collected a female with a shelled egg ready to be laid (nominate South African race), but neither published a description of these authentically identified eggs.

Nothing is known of the number of eggs laid in one season by one female, of any individual specificity in hosts, or of the interval between eggs. The ovary of a trapped female that laid an egg just before dying, showed, on microscopical examination, one discharged follicle and five ova considerably enlarged. The largest of these was not more than half the size it should be for an egg ready for deposition of the albuminous layers, the next largest one was about half as large, and the others were much smaller. As far as such evidence may be used, the indications are that at least six eggs would have been laid, and that the interval between the one just laid and the next one would probably have been two days.

The eggs usually are laid in the nests of hole-nesting birds, as shown by the host records discussed further on in this report. As a rule only one egg is deposited in any one nest, but in at least one case two eggs were found in the same nest together with some of the host's eggs, as mentioned in the discussion of *Tricholaema leucomelan*, the pied barbet. In this instance it is not possible to say whether the two eggs were laid by the same hen or if two honey-guides laid in the same nest. The two eggs were similar enough in size (20 by 16.6 and 20 by 15.6 mm.) to have been the product of a single hen. Aside from the fact that the barbet's eggs are somewhat different in size from those of the honey-guide, there is a noticeable difference in the color of the eggs when freshly laid due to the fact that the yolk of *Indicator minor* is pale yellow whereas that of the barbet is very reddish.

When the honey-guide is ready to lay it seems quite indifferent to the attacks and protestations of the intended victims. If driven away, it persistenly returns until it finds an opportunity to get into the nest hole, which it then does promptly. Judging by the number of times people have seen honey-guides trying to get into these nests, especially of barbets of several species, it would seem that egg laying (if most of these attempts are preliminary to egg deposition) is not restricted to the very early morning hours as in so many other birds. It may also be due, in part at least, to the fact that usually one of the pair of barbets remains on guard in or near the nest when the other is away, making it difficult for the parasite always to be finished laying as early as might otherwise be the case. (For accounts of such attempts at entry, see under the various host species.)

It is puzzling to try to explain the persistence with which lesser honey-guides keep trying to enter or, at least, look into nest holes of the birds they victimize. They do so more frequently (or, to be more accurate, they have been seen doing so more frequently) than the greater honey-guide, *I. indicator*. They have been known to "visit" barbet's nests containing well incubated eggs and even chicks, none of which were honey-guides—in other words, nests in which they had not laid. Skead (1951, p. 53) records one instance in which a lesser honey-guide came into his garden where a pair of black-collared barbets were living. This was in September, when the barbets were neither nesting nor using the holes in the trees there for sleeping. The pair of barbets was feeding at the time and immediately reacted towards the honey-guide, shrieking loudly, something they ordinarily do not do to other birds. The honey-guide was in no way perturbed by this, and in spite of the screams of the birds it casually looked into the old barbet nest as it passed. This habit of looking into nest holes may be responsible for the erroneous statement in the literature to the effect that the honey-guides show a certain amount of interest in their young while the latter are still in the nests of the fosterers. There is no evidence that they attempt to do anything for their young.

One observation of Gilges (1939) suggests that the nests in which the eggs are laid may be located in advance and visited some time before an egg is actually ready to be laid. Gilges found a lesser honey-guide trying to enter a nest of a black-collared barbet, *Lybius torquatus*, only to be driven off repeatedly by the owners. It was so persistent that Gilges felt it probably had an egg ready to be laid. He shot it and found to his surprise that none of the ova was within many days of being ready.

As far as the still meager data permit one to draw a conclusion, it seems that the honey-guide does not necessarily remove one of the host's eggs when laying its own in the nest. In support of this statement I may point out that out of 14 parasitized nests of the black collared barbet, each with a single egg of the parasite, the number of the barbet's eggs was 4 in each of four nests, 3 in each of five nests, 2 in each of four nests, and 1 in one nest. The usual clutch of the barbet in nonparasitized nests is 3 or 4 eggs. Those nests in which the barbets' eggs were only 2 or 1 in number may have been nests in which laying had not been completed. However, in at least one instance we have data showing that a barbet's egg was removed, and, inferentially, that it probably was done by a honey-guide. The facts are as follows: Ranger found a black-collared barbet's nest containing 4 eggs of the barbet on November 2; on November 9 he reinspected it and found only 3 of the barbet's eggs and 2 of the lesser honey-guide's. The apparent implication is that the missing barbet egg was removed when one of the parasitic eggs was deposited, although the second honey-guide egg was not laid at the expense of still another barbet egg.

I know of no instance in which the host's eggs were punctured or otherwise damaged by the lesser honey-guide. This is rather surprising when one considers that in the greater honey-guide, *Indicator indicator*, egg puncturing is very frequent.

That the parasite does not always "time" its laying too well is indicated by a case reported to me by Mr. Robin Guy. Near Pietermaritzburg, Natal, in November 1945 he found a nest of a black-collared barbet containing 4 eggs of the host and 1 of the honey-guide. On blowing the eggs he found that the barbet eggs were in an advanced stage of incubation while the honey-guide egg was fresh.

The incubation period needs further study. It has been estimated by Skead (1951, pp. 53–55) as about 16½ days (in a nest of *Lybius torquatus*): but more recently Ranger found it to be not more than 12 days, and possibly only 11 (in a nest of the same host species)—at least it was determined to have begun and ended within a period of 12 days.

Hosts or Victims

The known victims of the lesser honey-guide number 21 species, or, including races, 28 forms of birds. With the single exception of one record of a swallow, all the hosts are hole-nesting birds, and the swallow in question makes a cup-shaped nest under a ledge or roof, so it is, if not a hole-nester, at least a nester in dark places. The majority of the victims are barbets (9 species, or 16 species and subspecies). Out of a total of something over 50 definite records of nests containing eggs or chicks of *Indicator minor*, 35 are barbets' nests; and there are 15 or 20 more indefinite records of barbet hosts in my files. Of the definite records, two records have to do with one species of bee-eater, two with a kingfisher, five with five forms of woodpeckers (only one instance for each of these birds), three of tits, and single instances are at hand of parasitism of single species of swallows, starlings, and weaver finches. As in the case of the greater honey-guide, the list of hosts is bound to be increased as more field data become available. From vast areas of Africa inhabited by the lesser honey-guide, in its various races, there are as yet no host records at all. Although it is, therefore, impossible to say which species in general are most frequently chosen by the parasite, it does seem that the barbets, as a group, are the favorite hosts. At present the black-collared barbet, *Lybius torquatus* (and races), is easily the victim most frequently recorded, with 15 actual instances and at least as many more indefinite ones.

Melittophagus pusillus meridionalis Sharpe. Lesser bee-eater.

Melittophagus meridionalis Sharpe, Catalogue of the birds in the British Museum, vol. 17, pp. 44 (in key), 45, pl. 1, fig. 4, 1892. ("Southeastern Africa from Natal to the Zambesi, and thence to the Zanzibar district on the east coast and to Angola and the Lower Congo on the west"; restricted type locality: Pinetown, Natal.)

In the Carlisle collection in the National Museum of Southern Rhodesia are six sets of eggs of this bee-eater, all from Strathmore, Southern Rhodesia, each containing a single egg ascribed to *Indicator minor.* Two of these clutches have 3 eggs each of the barbet, one has 2, and the other three have only single eggs of the host. The dates of these sets are October 10, 10, 10, 12, 24, and November 19. The honey-guide eggs, measured for me by Mr. R. H. N. Smithers of the National Museum of Southern Rhodesia, are, in some cases, either large eggs of *minor* or small ones of *indicator,* but in at least two of these sets they are too small to be *indicator,* 19.9 by 15.9 and 22.6 by 17 mm. These two, at least, seem safe to accept as *minor.*

The lesser bee-eater is a common host of the greater honey-guide, but aside from these Strathmore records I know of no evidence that it also serves in this capacity for the lesser honey-guide.

Halcyon chelicuti chelicuti (Stanley). Striped kingfisher.
Alaudo chelicuti Anonymous=STANLEY, *in* Salt, Voyage to Abyssinia . . ., App. 4, p. lvi, 1814. (Chelicut, Ethiopia.)

The striped kingfisher is parasitized by the lesser honey-guide in South Africa, but apparently not commonly, as only two instances of its being so affected are known to me. A. Roberts (1939, pp. 102–105) records both—a set of four eggs of the kingfisher and one of the parasite taken at St. Lucia Lake, Zululand, October 20, 1931, and a set of three eggs of the kingfisher and one of the honey-guide collected at Mokeetsi, Transvaal, December 10, 1930. Both sets are now in the Transvaal Museum. These are apparently the same records as those listed by Priest (1948, p. 64).

Gymnobucco bonapartei bonapartei Hartlaub. Bonaparte's brown barbet.
Gymnobucco bonapartei HARTLAUB, Journ. Ornith., vol. 2, p. 410, 1854 (Gaboon.)

At Bitye, Cameroons, April 1, Bates (1909a, p. 16) found a chick of the lesser honey-guide (*Indicator minor conirostris*) in a nest of Bonaparte's brown barbet. "In other holes in the same dead tree were birds of that species [*Gymnobucco*]; but the little *Indicator* was found in its hole alone, so that it formed, apparently, the entire family of its foster-parents." Bannerman (1953, p. 727) also lists this barbet as a host of *I. m. conirostris.*

At Lukolela, Belgian Congo, on December 12, 1930, Chapin (1939, pp. 512, 544–545) examined a large dead tree occupied by a nesting colony of this barbet. He saw five of these honey-guides in the vicinity, and one of them even flew up to and clung to the lower edge of a nesting entrance. He collected two of the honey-guides and found one to be a male with slightly enlarged gonads; the other was a female with a soft egg in the oviduct. Nine weeks later the barbets were still busy at their nests, and one honey-guide was seen in a nearby tree.

Stactolaema olivacea olivacea (Shelley). East African olive barbet.
Barbatula olivacea SHELLEY. Ibis, 1880, ser. 4, vol. 4, p. 334, pl. 7. (Rabbai, near Mombasa, Kenya Colony.)

Van Someren informs me (in litt.) that he has found single nestling lesser honey-guides in each of three or four nests of this barbet in the coastal areas of Kenya Colony in May and June. Once he flushed an adult lesser honey-guide from a nest of an olive barbet and found the nest to contain an egg of the parasite together with two eggs of the host.

Stactolaema anchietae (Bocage). Yellow-headed barbet.
Buccanodon anchietae BOCAGE, Proc. Zool. Soc. London (1869), p. 436, pl. 29, 1869. (Caconda.)

Two subspecies of this barbet are reported as victims of the lesser honey-guide, each one a single time.

A most remarkable set of eggs of the Nyasaland race *Stactolaema a. whytii*[42] was taken at Blantyre, Nyasaland, October 12, 1921, by Sir Charles F. Belcher. According to Benson (1952a, p. 444) there were three eggs of the barbet, three of the scaly-throated honey-guide, and one of the lesser honey-guide. The identification of the last seems fairly safe, on size characters. (See under *I. variegatus*, p. 104, for further discussion.)

One record for the Mashona race *S. a. sowerbyi* Sharpe[43] is known to me—a set of three eggs of this barbet with one of the lesser honey-guide collected at Marandellas, Southern Rhodesia, October 10, 1948, by B. M. Neuby-Varty and now in the collection of Mr. C. H. Jerome, Estcourt, Natal. I am indebted to Mr. Jerome for this information.

Pogoniulus pusillus pusillus (Dumont). Red-fronted tinkerbird.
Bucco pusillus DUMONT, Dictionnaire des sciences naturelle, ed. Levrault, vol. 4, p. 50, 1816. (Sandag [i. e., Sundays] River, Swart Kop River and in the Karrou, Cape Province.)

This bird is listed as a victim of the lesser honey-guide by Layard (ed. Sharpe, 1875–1884, pp. 169–170) on the authority of Mrs. Barber. Sparrow (1936, p. 5) also lists it, but whether he had any data other than Layard's is not clear.

Pogoniulus bilineatus (Sundevall). Golden-rumped tinkerbird.
Megalaema bilineata SUNDEVALL, Öfv. Svenska Vet.-Akad. Förh. (1850), p. 109, 1850. (Lower Caffraria, i. e., Natal.)

The small size of this barbet and of its nest hole would seem to render it poorly fitted to be a host of the lesser honey-guide, and, indeed, there is some reason to question the identification of the honey-guide chicks found in the nests of two races of this little barbet. One cannot help but wonder if they may not have been nestlings of *Indicator exilis*.

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[42] *Smilorhis whytii* Shelley, Ibis, ser. 6, vol. 5, p. 11, pl. 1, 1893. (Zomba, Nyasaland.)

[43] *Stactolaema sowerbyi* Sharpe, Bull. Brit. Ornith. Club, vol. 7, p. xxxvi, 1898. (Mashonaland, i. e., Fort Chiquequa, ex Ibis, 1898, p. 572.)

The Gaboon race of this tinkerbird, *P. b. leucolaima* (J. and E. Verreaux),[44] is recorded provisionally as a host of the lesser honey-guide (*I. minor conirostris*?) on the basis of one record, a chick of the parasite found in a nest of the little barbet at Bitye, Cameroons, by Bates (1911, p. 503), who writes that a "nestling *Indicator*, probably *I. conirostris*, has been found in the hole of a . . . *Barbatula leucolaema*. The old Barbet was caught in the hole with it, but there was no other nestling. The hole had the entrance just the size of an average finger-ring, and much too small to admit a grown Honey-guide of this species. The egg may, of course, have been carried and dropped into the hole by the bird with its bill. It is a harder problem to explain how the young Honey-guide could ever have got out of the hole if it had remained till it grew larger." Chapin (1939, pp. 544–545) also expressed some doubt that this nestling was *I. minor* and not *I. exilis*, as does also Bannerman (1933, pp. 413–415).

Van Someren writes me that he once took a young lesser honey-guide (*I. minor minor*) from a nest of this little tinkerbird (subspecies *jacksoni* (Sharpe) [45] in western Kenya Colony. I know of no other instance, and cannot help but wonder if the honey-guide may not have been *I. exilis meliphilus*, purely on the argument that the nest-hole must have been very small for the lesser honey-guide. However, the fact that the equally small *P. pusillus* has been reported as a host of *I. minor* in South Africa, where no race of *I. exilis* occurs, makes it not impossible that van Someren's identification is correct after all.

Tricholaema leucomelan **(Boddaert).** Pied barbet.

Bucco leucomelas BODDAERT, Table des planches enluminéez d'histoire naturelle, p. 43, 1783. (Cape of Good Hope, ex Daubenton, Planches enluminées, pl. 688, fig. 1.)

This barbet is widely parasitized throughout southern Africa, and at least four subspecies have been found to be victimized by the lesser honey-guide. The nominate race, found in the Cape Province, the Karroo, and the Orange Free State, was first reported as a host of the lesser honey-guide by Layard (1867, p. 243), possibly on the basis of Atmore's observations. Haagner and Ivy (1907b, p. 103) record an egg of this honey-guide from a pied barbet's nest found in the Albany division, Cape Province. Sparrow (1936, p. 5) lists the pied barbet as a fosterer, but it is not clear if he based his statement on Layard, and Haagner and Ivy, or on new, unpublished data.

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[44] *Barbatula leucolaima* J. and E. Verreaux, Rev. et Mag. Zool., ser. 2, vol. 3, p. 263, June 1851. (Gaboon.)

[45] *Barbatula jacksoni* Sharpe, Bull. Brit. Ornith. Club, vol. 7, p. vii, 1897. (Mau, Kenya Colony.)

Near where Haagner and Ivy made their observation at Bedford, in the eastern Cape Province, Pringle (in litt.) has found eggs of *Indicator minor* in many nests of the pied barbet. Usually there was but one of the honey-guide's eggs in a nest with two or three of the host. On one occasion he found two eggs of each in the same nest. I am much indebted to him for the following, more detailed descriptions that he sent to me. At Bedford on October 14, 1947, he found two parasitized nests of this barbet; one nest had one egg and the other had two eggs of the lesser honey-guide. All the honey-guide eggs were fresh. On another occasion, as he approached the nesting hole of a pied barbet in a dry aloe stump, he noticed a barbet in the entrance and a lesser honey-guide in a tree some 15 yards away. He came up to within about 3 yards of the nest before the barbet flew out, and immediately thereafter the honey-guide flew in. The barbet then went in after the intruder and dragged it (her ?) out, having gripped it by the back of the neck. As an experiment Pringle then chased off the barbet each time when it came back to the nest, and the honey-guide made repeated attempts to enter the nest hole each time the barbet was driven off. Invariably the parasite was attacked immediately by the barbet. This was kept up for fully half an hour, but without success for the honey-guide, which then finally flew away. During all this time Pringle saw only one honey-guide and felt satisfied that it was always the same individual.

On still another occasion Pringle found a pied barbet's nest containing three eggs of the barbet and one of the lesser honey-guide. This nest also was in a hole in an aloe. It was left for observation. When the honey-guide egg hatched, the other eggs (or chicks) disappeared. When Pringle examined the nest "the honey-guide chick was then not yet a day old, and yet I could find no trace of eggshells below the nest. This stump was practically perpendicular and the hole fully 12 inches deep."

If the young honey-guide was really not yet a day old, it would seem that the eviction of the other contents of the nest might have been done by the barbets and not by the young parasite. Yet there is no reason to which one might attribute any such presumed action on their part.

It is possible that these records from the eastern Cape Province may prove eventually to refer not to typical *leucomelan* but to the race *affinis*. Material to decide this point is not available to me. A. Roberts (1940, p. 177) and Jack Vincent (1952, p. 49) record *affinis* from the eastern Cape Province, while Peters (1948, p. 52) limits *affinis* to Natal.

A. Roberts (1939, pp. 102–103) states that in the collections of the Transvaal Museum there is a set of three eggs of this bird (subspecies *zuluensis* (Roberts) [46]) with one of the lesser honey-guide. This set was collected at Ingwavuma, Zululand, November 12, 1933.

Plowes collected a set of three eggs of the barbet with one of a lesser honey-guide at the Matopos Research Station, Southern Rhodesia. The set is now in the collection of the National Museum of Southern Rhodesia in Bulawayo.

Near Moorddrift, Transvaal, on December 11, 1924, a native showed me a nesting hole of the pied barbet (subspecies *centralis* (Roberts) [47]). In it were three eggs of the barbet and one egg of a lesser honey-guide, all of which were left for further observation but which perished due to the predatory action of a snake two days later.

A. Roberts (1913, p. 21) saw a lesser honey-guide trying to enter a pied barbet's nest only to be driven off by one of the pair of barbets. After this was repeated several times, he shot the honey-guide and found it to have a shelled egg in the oviduct. It seems safe to assume it would have laid this egg in the barbet's nest if it had been able to.

The late H. W. Bell-Marley informed me that he found the pied barbet to be parasitized by the lesser honey-guide on several occasions in central Natal. The race of the host in that area is *affinis* (Shelley).[48]

Tricholaema diadematum massaicum **(Reichenow).** Masai red-fronted barbet.

Pogonorhynchus massaicus Reichenow, Journ. Ornith., vol. 35, p. 59, 1887. (Loeru, Tanganyika Territory.)

All that I know of the red-fronted barbet as a victim of the lesser honey-guide is that van Someren writes me that he has often seen the latter at nest holes of this barbet. He has collected nestling lesser honey-guides from such nests (one in each nest) in the Ngong area, Kenya Colony, from April to July; in the near vicinity of Nairobi he found similar lone nestlings in several nests in May and August. It would seem that the red-fronted barbet is probably a frequent host of the lesser honey-guide.

Fuggles-Couchman and Elliott (1946, p. 335) saw an *Indicator minor* acting in a very inquisitive manner about a nest of a Masai red-fronted barbet near Monduli, Tanganyika Territory, on January 30. The honey-guide was finally "chased off by the agitated barbets only with great difficulty."

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[46] *Notopogonius leucomelas zuluensis* Roberts, Ann. Transvaal Mus., vol. 14, pp. 237, 240, 1931. (Mkuzi River, east of Ubombo, Zululand.)

[47] *Notopogonius leucomelas centralis* Roberts, Ann. Transvaal Mus., vol. 15, p. 26, 1932. (Rustenberg, Transvaal.)

[48] *Pogonorhynchus affinis* Shelley, Proc. Zool. Soc. London (1879), p. 680, 1880. (Weenen, Natal.)

Lybius torquatus (Dumont). Black-collared barbet.

Bucco torquatus Dumont, Dictionnaire des sciences naturelle, ed. Levrault, vol. 4, p. 56, 1816. (Brazil, error=South Africa; Goffin, Muséum d'Histoire Naturelle des Pays-Bas, Revue Méthodique . . ., No. 15, Buccones, p. 4, 1863.)

At least three races of this species are known to be victims of the lesser honey-guide, but inasmuch as most of the records pertain to the South African race, the discussion will be given here for the whole species and only the actual records outlined under the other two subspecies.

The black-collared barbet is the most frequently reported host of the lesser honey-guide from the vicinity of Lake Mweru and Nyasaland south to the Cape Province. Some 15 definite records and at least as many more indefinite ones have come to my attention.

Ivy (1901, pp. 21–22) saw a lesser honey-guide trying to enter a nesting hole of one of these barbets in the eastern Cape Province. It was driven off by the male barbet which was joined shortly by its mate. In about five minutes the *Indicator* returned and the episode was repeated many times for about an hour in all. The honey-guide then was shot and was found to have an egg protruding from the vent. In the barbet's nest were two barbet eggs.

Other observers have recorded similar occurrences. Thus, Gilges (1939) on the Umtata River, Transkei, Cape Province, watched a lesser honey-guide attempting to enter a nest of this barbet. "While one of the Barbets was sitting in the nest, the other partner very noisily tried to chase the intruder away, in which . . . it did not succeed. Watching the persistency of the Honeyguide, which . . . favours the Black-collared Barbet as the future foster parent of its offspring, for over 20 minutes, we came to the conclusion that a fully developed egg was about to be deposited. The examination of the specimen later showed, however, that none of the eggs was bigger than a lentil. Apparently the bird marks the nest down in advance . . ."

To take another instance, this time from Dowa, Nyasaland, Benson (1940, pp. 429–430) on October 9 watched "a *Lybius torquatus* with just its head protruded out of a hole in a tree, watching the scene now to be described, while another *Lybius torquatus* was doing its utmost to keep an *Indicator minor* away from the hole. The Honey-guide would alight on a branch near the hole, only to be immediately driven away. The Barbet would keep up a scolding note all the time, rather like the chatter of a *Turdoides jardinei*. Finally the Honey-Guide would fly right away, hotly pursued by the Barbet. Three days later this same performance was again witnessed, except that this time there was no Barbet in the hole, and the Honey-Guide succeeded in entering it. Presumably it wished to lay its egg in the Barbet's nesting-hole."

On two other occasions in the same month Benson saw a lesser honey-guide in flight closely pursued by a black-collared barbet.

Writing of this barbet and the white-eared barbet in northern Zululand, Roberts (1930a, p. 25) observed that they were being "much pestered in late October and early November by the attention of the Lesser and the Variegated Honeyguides, one or other of these species always awaiting an opportunity to enter the Barbet nests and deposit its egg there, but being warded off every time by the male Barbet on guard. The noisy chattering of the Honeyguide and the angry gutteral expostulations of the Barbet in pursuit . . . quite commonly attract attention. How often the Honeyguide succeeds is difficult to estimate, but judging by the quantity of Barbets and complete nests with young that were observed, the persistence of the Honeyguide is seldom rewarded."

Judging by the number of parasitized nests of the barbet it would seem, however, that the lesser honey-guide succeeds often enough in its endeavors. Thus, in a later paper Roberts (1939, pp. 102–105) lists three parasitized sets of eggs in the Transvaal Museum; one from Port Shepstone, Natal, February 27, 1922, containing four eggs of the host and one of the parasite; one from Hilton, Natal, November 17, 1926, with two eggs of the barbet and one of the honey-guide; and one from St. Lucia Lake, Zululand, December 1, 1920, also with two eggs of the victim and one egg of the parasite. He further mentions a set of three eggs with one of the honey-guide from Mokeetsi, Transvaal, December 6, 1922, another from Umzumbi, Natal, February 2, 1922, with the same number of eggs, and a set of two eggs with one of the honey-guide reported by Haagner and Ivy (1907b, p. 103, pl. 4). Other records are a set of four eggs of the barbet and one of the honey-guide collected by A. D. Millar at Palmiet, December 17, 1899 (Chubb, 1914, p. 63); a nest with a single honey-guide chick found the same place and date (Stark and Sclater, 1903, p. 154); a set of one egg each of the host and the parasite, Kronitz Kloof, Natal, December 4, 1903 (Sparrow, 1936, p. 5); one set from Petermaritzburg, Natal, late October, with two eggs of the barbet and one of the honey-guide, and another set from the same area in November with 4 eggs of the barbet and one of the parasite (Robin Guy, in litt.). Recently Plowes informed me that at the Matopos Research Station, about 20 miles from Bulawayo, Southern Rhodesia, on October 30 he found an egg of *Indicator minor* in a nest of a black-collared barbet containing four eggs of the barbet (this set is now in the National Museum of Southern Rhodesia), and on November 30 he found another parasitized nest of the same barbet.

Priest (1948, p. 64) lists five parasitized nests, apparently the same as those listed by Roberts. In addition to these, another may be noted—an egg of the lesser honey-guide taken from a nest of this barbet at Wedza, November 11, 1930, by Captain Priest and now in the collection of the Victoria Memorial Museum at Salisbury.

Skead (1951, pp. 53–55) found the lesser honey-guide to parasitize this barbet at "Gameston," 15 miles southwest of Grahamstown, Albany district, Cape Province. The nest contained three eggs of the host and one of the parasite, and when first found on September 29 it contained only the first barbet egg. On October 17, three of the eggs hatched; the last one hatched the next morning. On October 25 the nest contained only a single chick, the young honey-guide. In other words, between October 17 and 25 the three young barbets disappeared. Inasmuch as one or the other of the barbets was always in the nest it was impossible to see just what happened and when. Further details of the development of the young honey-guide are described from this case and another from Umtaleni, near Kei Road, in our discussion of the nestling stage of the parasite.

To the above data may be added that B. M. Newby-Varty found the black-collared barbet to be victimized by the lesser honey-guide on at least three occasions near Marandellas, Southern Rhodesia. The records are as follows: one nest with three eggs of the barbet and one of the parasite, all eggs fresh, October 20, 1946; another also with three eggs of the host and one of the honey-guide, slightly incubated, late October, 1946; and one with a three-fourths grown young lesser honey-guide as its sole occupant, early in November.

From Nyasaland, where the birds approach the subspecies *zombae* (Shelley),[49] we have the following data. Benson (1952a, p. 445) collected a set of three eggs of this barbet with one of the lesser honey-guide at Mkhoma, Nyasaland, October 22, 1950; all the eggs were still fresh. As mentioned earlier, the same observer (1940, pp. 429–430) saw a lesser honey-guide enter a black-collared barbet's nesting hole after many unsuccessful earlier attempts, but he was unable to examine the nest to see if the parasite actually laid an egg in it. However, the apparent importance of this host in the economy of the honey-guide is hinted at by Benson in a later paper (1942, p. 300) when he tries to account for the absence of the latter bird in western Nyasaland by the local absence of the barbet.

A nest with two eggs of the barbet and one of the lesser honey-guide, near Lake Mweru, October 13, is reported by A. W. Vincent (1946, pp. 321–322). The record refers to the subspecies *congicus* (Reichenow).[50]

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[49] *Melanobucco zombae* Shelley, Ibis, ser. 6, vol. 5, 1893, p. 10. (Zomba, Nyasaland.)

[50] *Melanobucco torquatus congicus* Reichenow, *in* Werther, Die mittleren Hochländer des nördlichen Deutsch-Ost-Afrika . . . , p. 273, 1898. (Congo region; type from Malanje, Angola.)

Trachyphonus vaillantii vaillantii Ranzani. Levaillant's barbet.
Trachyphonus vailantii Ranzani, Elementi di zoologia, vol. 3, pt. 2, p. 159, 1821. (South Africa, ex Levaillant=southeastern Cape Province, fide Vincent, Bull. Brit. Ornith. Club, vol. 55, p. 94, 1935.)

Two parasitized sets of eggs are in the collections of the Transvaal Museum (A. Roberts, 1939, pp. 102–105): one from Plumtree, Southern Rhodesia, October 21, 1923, containing two eggs of the barbet and one of the honey-guide, and one from Mokeetsi, Transvaal, October 29, 1928, containing three eggs of the host and one of the parasite. These records are apparently the same as those listed by Priest (1948, p. 64).

Jynx ruficollis ruficollis Wagler. South African wryneck.
Jynx ruficollis Wagler, Naturliches System der Amphibien . . . , p. 118, 1830. (Kaffirland=Uitenhage, eastern Cape Province.)

One record.

A set of four eggs with one of the lesser honey-guide, taken at Umsonga, Natal, September 27, 1922, is now in the collection of the Transvaal Museum (Roberts, 1939, pp. 102–105). The same record appears to be the basis for the inclusion of the wryneck in the list of hosts given by Priest (1948, p. 64). A further suggestion of interest in this bird by the honey-guide is evidenced by the fact that near Kei Road, eastern Cape Province, Gordon Ranger once saw a lesser honey-guide perched in a tree close to an occupied nest of a wryneck. When the honey-guide flew off the two wrynecks chased it out of sight. Some 15 minutes later the honey-guide returned to the tree but made no attempt to get into the nest hole, and after a few minutes went off and disappeared.

Campethera nubica scriptoricauda (Reichenow). Southern Nubian woodpecker.
Dendromus scriptoricauda Reichenow, Ornith. Monatsb., vol. 4, p. 131, 1896. (Bumi, Tanganyika Territory; Peters, Check-list of birds of the world, vol. 6, p. 117, 1948.)

One record.

A nest containing two eggs of this woodpecker and one of the lesser honey-guide was collected at Chiromo, Nyasaland, November 4, 1921, by C. F. Belcher (Benson, 1952a, p. 444).

Campethera abingoni abingoni (A. Smith). Abingon's golden-tailed woodpecker.
Chrysoptilus abingoni A. Smith, Report of the expedition for exploring central Africa, p. 53, 1836. (Port Natal; i. e., Durban, Natal.)

One uncertain record, the uncertainty being the identification of the parasite.

Two eggs of Abingon's woodpecker with one probably of a lesser honey-guide were taken by Belcher (1930, p. 168) at Nyambadwe, near Blantyre, Nyasaland, September 29, 1926. The honey-guide egg measured 20.5 by 17.5 mm., which dimensions agree with those of *I. minor* eggs. In his most recent publication, Benson (1953, p. 45) accepts this identification.

Dendropicos fuscescens natalensis Roberts. Zulu cardinal woodpecker.

Dendropicos hartlaubi natalensis Roberts, Ann. Transvaal Mus., vol. 10, p. 84, 1924. (Red Hill, Natal.)

I know of only a single instance of the cardinal woodpecker being parasitized by the lesser honey-guide.

A. Roberts (1936, p. 193) found a young honey-guide (which he believed to be *I. minor minor*) in a nest of this bird on the Mkusi River, Zululand. This seems to be the same record as the one he refers to in an earlier paper (1930a, p. 25).

Mesopicus griseocephalus griseocephalus (Boddaert). Olive woodpecker.

Picus griseocephalus Boddaert, Table des planches enluminéez d'histoire naturelle, p. 49, 1783. (Cape of Good Hope, ex Daubenton, Planches enluminées, pl. 786.)

One case has come to my attention.

Layard (1867, p. 243) records this woodpecker (under the name of *Picus capensis*) as a victim of the lesser honey-guide, but gives no further information. Sparrow (1936, p. 5) lists the olive woodpecker as one of the known hosts, possibly on the basis of Layard's statement.

Hirundo albigularis Strickland. White-throated swallow.

Hirundo albigularis Strickland. *in* Jardine, Contributions to ornithology, text p. 17, pl. 15, 1849. (South Africa.)

One record.

A. Roberts (1939, pp. 102–103) reports a set of two eggs of this swallow with one of the lesser honey-guide, collected at Umzumbi, Natal, December 12, 1920, now in the collections of the Transvaal Museum.

This is the only bird among the victims of the lesser honey-guide that does not breed in a hole or in a completely enclosed nest. Priest (1948, p. 102) describes the nest as a deep cup made of pellets of mud, lined with grass and feathers, and built under a ledge or culvert or on the rafters of an old barn.

Parus afer parvirostris Shelley. Mashonaland gray tit.

Parus afer parvirostris Shelley, Birds of Africa, vol. 2, pp. 225, 241, 1900. (Salisbury.)

Two probable but not wholly certain records.

Priest (1936, p. 99) records a pair of these tits feeding a young fledgling lesser honey-guide in his garden at Wedza on November 15 and states that three years previous to this he "obtained an egg of *I. m. minor* from a nest of this tit in a hole in a tree, also in my garden. It was about November 15th that I heard a loud and oft repeated *chirri-chirri-chirri . . . chirri-chirri-chirri.* I went out and saw this greedy young rascal of a Honey-guide being waited on 'bill and foot' by the Tits; the more they fed him the louder and more incessantly did he scream for more. This went on for four or five days when his screams ceased, and he took himself to the bush."

Later (p. 102) in discussing the black tit, *Parus niger*, he writes that one set of eggs "like the Grey Tit's, also contained the white egg of a Honey-guide; I think, *I. indicator*, but on that point I cannot speak with assurance." Priest's account leaves much to be desired as to definiteness. Whether there was a single young honey-guide or two of them, whether any young gray tits grew up in the same nest, and whether the species of parasite was *I. minor* or *I. indicator* are all unclear.

Parus niger niger Vieillot. Southern black tit.

Parus niger VIEILLOT, Nouveau dictionnaire d'histoire naturelle . . . , new ed., vol. 20, p. 325, 1818. (Africa; Sondag [= Sundays] River, eastern Cape Province, ex Levaillant, Histoire naturelle des oiseaux d'Afrique, vol. 3, pl. 137, 1802.)

One uncertain record.

Capt. Cecil D. Priest informs me that at Wedza, Southern Rhodesia, he once found a nest of the black tit containing an egg of the lesser honey-guide. This is the only record known to me. However, in his book on the birds of Southern Rhodesia (1936, p. 102) he writes of this record as pertaining to the greater honey-guide, *I. indicator.*

Cinnyricinclus leucogaster verreauxi (Bocage). Southern violet-backed starling.

Pholidauges verreauxi BOCAGE, *in* Finsch and Hartlaub, Die Vögel Ost-Afrikas, *in* Baron C. C. von der Decken's Reisen in Ost Afrika in 1859–61, vol. 4, p. 867, 1870. (Caconda.)

This handsome starling is known as a host of the lesser honey-guide on the basis of one record.

A set of three eggs of the starling with one of the parasite was collected at Mokeetsi, Transvaal, October 20, 1928, and is now in the collections of the Transvaal Museum, according to A. Roberts (1939, pp. 102–105). The same record is listed by Priest (1948, p. 64).

Petronia superciliaris (Blyth). South African rock sparrow.

Gymnorhis superciliaris BLYTH, Journ. Asiatic Soc. Bengal, vol. 45, p. 553, 1845. (South Africa.)

Known as a victim of the lesser honey-guide only in the eastern Cape Province. Victor Pringle informs me that at Bedford on many occasions he found the honey-guide at or near nests of this sparrow, and once he found a young *Indicator minor* in one of these nests.

Aside from the species discussed above as hosts of the lesser honey-guide, it may be mentioned that Godfrey (1912, p. 11) found an egg in a nest of a larger stripe-breasted swallow, *Hirundo cucullata*, at Pirie, Buffalo River Basin, eastern Cape Province, which he could not identify with certainty but which he presumed was deposited by a lesser honey-guide. Inasmuch as this swallow is known to be victimized by *Indicator indicator*, it would seem possible that the greater honey-guide was involved in this instance, but the record remains unidentifiable. In a later paper Godfrey (1930) writes that the lesser honey-guide lays in the nest of this swallow, but whether this is merely an uncritical acceptance of his earlier doubtful statement or whether he had accumulated additional evidence in the intervening years is impossible to say.

Questionable Host Records

Another bird not yet definitely known to be parasitized but which may well be so affected is the white-eared barbet, *Stactolaema leucotis leucotis* (Sundevall). Roberts (1930a, p. 25) noted lesser and variegated honey-guides trying to enter nest holes of this species in northern Zululand. In Tanganyika Territory the Moreaus (1937, pp. 173–174) similarly saw lesser honey-guides trying very persistently to enter nests of white-eared barbets (subspecies *kilimense* Shelley). Lack (1936, p. 825) also witnessed lesser honey-guides making repeated attempts to enter nests of this barbet at Amani, Tanganyika Territory, August 15 and 30.

Still another barbet, the naked-faced barbet *Gymnobucco calvus calvus* (Lafresnaye), is also probably parasitized but cannot be said to be recorded definitely as a host species, only inferentially so. In this case the data all have to do with the subspecies *Indicator minor pallidus* in Nigeria. Marchant (1950, p. 25; 1951, p. 73) writes that the honey-guide was never met with except at the breeding colonies of *Gymnobucco calvus*, "which species it evidently parasitized." At these colonies, from about January to May, one or two of the honey-guides could almost always be found. They were never actually seen to enter one of the nest holes as the barbets invariably drove them off. Apparently the sight of a honey-guide was enough to alarm the barbets, which then immediately flew after it and chased it away.

Bannerman (1951, p. 348) on the basis of Marchant's statement repeats the probability of this barbet being the host of *Indicator minor pallidus*.

One woodpecker has also been recorded—too uncertainly for inclusion in our list of hosts—as a victim of the lesser honey-guide. Captain Pitman writes me that he received from C. W. Benson a single egg of *Campethera b. bennettii* (A. Smith), Bennett's woodpecker, collected at Mzimba, Nyasaland, October 13, 1948. "It measures only 18.4 by 15.3 mm. and is far too small for the egg of this woodpecker, and I suspect it to be that of *Indicator minor*." Benson (1951, p. 91) later suggested that the egg might have been laid by *Prodotiscus insignis*, while still later (1952b, p. 151) he considers that *I. minor* may have been responsible, but from his wording it appears that he had in mind to say *I. exilis meliphilus*. In his latest publication (1953, p. 45) he lists Bennett's woodpecker as a host of *I. exilis meliphilus* without further comment.

At Entebbe, Uganda, Captain Pitman saw a lesser honey-guide being chased repeatedly by a pair of gray woodpeckers (*Mesopicus goertae*) from their breeding tree. This species of woodpecker is not yet recorded as a host of this honey-guide.

The early statements of the Verreaux brothers as to the lesser honey-guide parasitizing puff-backed shrikes, bulbuls, orioles, etc., are not to be taken seriously.

Nest Life and Development

The following account is based on two main sources—Skeads' published observations (1951, pp. 53–55) and Ranger's more recent ones (not yet published at the time of the present writing). Both were made in the eastern Cape Province—Skead's near Grahamstown, and Ranger's near Kei Road. In both cases the hosts were black-collared barbets. In the nest watched by Skead there were originally three eggs of the host and one of the parasite; in the one described by Ranger there were three eggs of the host and two of the honey-guide. In the former nest all four eggs hatched within a period of 12 to 24 hours; in the latter nest, one honey-guide egg hatched, followed two days later by the hatching of one of the barbet's eggs, while the other eggs did not hatch at all. Skead was unable to examine the young honey-guide for the first six days after it hatched as one of the pair of barbets was always on guard in the nest, but Ranger was able to make daily notes from the second day onwards.

As will be noted at the proper places, the two accounts do not agree in all particulars. Because no further data are available both are discussed, but on the whole it appears that Ranger had more detailed evidence on these points of difference than did Skead.

The actual hatching of a honey-guide's egg has not yet been watched. In fact, the only description of a day-old bird is Skead's statement to the effect that it was blind, naked, and pinkish. While there is no reason to doubt this (except for the color, which Ranger found to be whitish rather than pink in a 2-day-old bird), it should be noted that Skead's description was based on only slight examination of a bird in a deep nest hole seen with a mirror and a small light. It would seem that Ranger's more detailed description of a 2-day-old bird might give a more accurate picture of the newly hatched lesser honey-guide.

2ND DAY: The bird's bill was still so soft and pliable as to give the nestling the appearance of having not so much a definite beak, as in the young of most other birds, but rather a "snout." The illustrations of the 3-day-old bird (pl. 5) show the condition of the bill very well. The premaxilla and the mandible are terminated by sharp, narrow hooks of the same color as the rest of the "snout." The upper hook is much longer than the mandibular one, curved, but not reflexed. The mandibular hook is reflexed or bent backward as well as being curved. When the bill is closed these hooks come to lie side by side, not one in front of the other. The distal one-third of the maxilla has a marked tomial curve away from the plane of meeting with the mandible, causing the mouth to remain open terminally when the proximal two-thirds of the jaws meet in closing. The nestling has a very prominent callosity studded with scalelike tubercles on the heel of its foot. The skin all over is whitish to pale cream, and is entirely bare of feathers; the eyes are closed and do not form a raised rotundity on the surface of the head; the nostrils are circular with a thickened, slightly raised rim. The bird's back is flat, but not hollow; the abdomen is very large and bulging. By contrast, the young barbet chick that hatched when the honey-guide was two days old was much smaller, with a light wine-colored skin, with no protruding abdomen, similarly devoid of feathers, and with a similarly prominent heel pad.

In order to observe them better, Ranger took the two nestlings out of the nest into his cupped hands. There the young honey-guide began to bite the barbet chick savagely in great grasping bites, the jaws widely opened in its attacks. This drew blood and caused the barbet to squeak and attempt to crawl away. Ranger's fingers were treated in the same way, gaping jaws closing upon the skin with appreciable force. He tested the power of the bite on more tender areas and found that his tongue was punctured by the maxillary hook. Ranger writes that the honey-guide's attack on the barbet was a quite ferocious, relentless gripping and biting. Blood specks covered the barbet nestling which showed signs of weakening. The young parasite also attacked the eggs in the nest but was not able to puncture them.

3RD DAY: When the nest was visited at 10:10 a. m. the adult barbet was brooding the two chicks. The young barbet was weak, with the bite marks (having coagulated blood under the skin) prominent on its back and abdomen. The nestling honey-guide was not engaged in biting at the time, but when Ranger replaced the two in the nest after examining them it again attacked the young barbet.

4TH DAY: Both chicks were still present. The young honey-guide measured 57 mm. from tip of bill to tip of rump (the barbet only 46 mm.); the maxillary hook 1.25 mm. long, the mandibular one .75 mm.; the width of the fully extended gape from end of premaxilla to the end of mandible 14 mm.; length of mouth or gape 7.5 mm.

5TH DAY: The barbet nestling was dead, reduced to an emaciated mass. It had been dead apparently for some hours as the collapsed abdomen was becoming green. The young honey-guide was thriving, the hooks appeared longer than before, the nostrils becoming distinctly tubular. The eyes began to show some blue through the sealed lids. The remiges were indicated by blue marks under the skin, and the rectrices as points. When placed in the hand the bird did bite against the fingers but was less active in this reaction than previously. The large abdomen rendered the bird awkward, but it could assume a balanced position with the aid of its legs, the two legs and the abdomen forming a tripod of sorts.

6TH DAY: The barbet nestling's body was gone. The young honey-guide was now developing a more distinct beak; the hooks appeared to be longer than originally, and in the closed bill the maxillary hook projected just below the lower surface of the end of the mandible. Due to the fact that the tomial edge of the maxilla was becoming straighter, the closed bill showed little of its original terminal gap. No feather sheaths were protruding as yet. When held in the hand the bird showed no inclination to bite the fingers. Its voice was a weak, wheezy whistle as in the beginning. The fact that the dead body of the barbet nestling was removed (probably by the adult barbets) by the sixth day is in keeping with what Skead noted in his account. In the nest he watched three eggs of the host and one of the honey-guide all hatched within 12 to 24 hours, but by the time the latter was a week old the three young barbets had disappeared.

9TH DAY: The tubular nostrils were assuming a forward projection; there was no change in bill color or in the body color except that the back was becoming pinkish. The feather sheaths of the main body tracts were out except on mantle, crown, and chin and were dark from upper neck to lower breast, the lateroventral areas pale yellow or cream; flanks also out. [It may be remarked that in Skead's published data the bird was still devoid of plumage on its 12th day and it was not until the 13th day that the quills began to appear through the skin. With only two "case histories" available it is difficult to account for this discrepancy. The divergence appears to be too great for what is considered a "normal" variability in developmental rate.]

10TH DAY: The groove between the eyelids was deepening, suggesting that the lids would part soon. Length of nestling with neck stretched, 3.3 inches; reposed, 2.75 inches.

11TH DAY: Eyelids were parted but kept closed; eyeballs did not bulge out of surface of head. Premaxillary tomium nearly meeting the mandibular one throughout, so that closed bill showed only slight open space. The maxillary hook thus projected well beyond the lower surface of the mandible. The remiges and rectrices (not out on the ninth day when the body tracts were found to have emerged) were now out, and protruded a little less than 1 mm. Hooks were tested by hand and found to be still firmly attached.

15TH DAY: Hooks and egg-tooth were no longer present. Not a vestige of any connecting tissue or scar was present at the tip of the maxilla, which was absolutely smooth and polished and with a "normal" tip (examined with a hand lens). The tip of the mandible retained an upturned stump, possibly the point of attachment of the lower hook. The tomial edges of the maxilla and mandible were now meeting throughout in the closed bill. The head was still relatively naked but feather sheaths were out although not erupted; all the other tracts were well out, those of the front of the neck and breast most advanced, followed in degree by the flanks; neck and breast uniform green-gray, posterior underparts cream color; the longest primaries 15 mm. long, the rectrices 5 mm. The tubular nostrils were directed forward; the eyelids maintained nearly closed. [In Skead's description the eyes were three-quarters open on the 14th day.]

16TH DAY: Eyelids still had not assumed the circular, completely open form. The nestling was given a test for its reaction to a nest mate. A glossy starling chick was placed beside it in the nest, and the honey-guide gave no reaction at all, even when the young starling lay partly upon it. It merely uttered its low wheezy cry. The young honey-guide voided dung which contained beetle elytra and fruit seeds about 4 mm. long.

Skead saw a 16-day-old honey-guide in the nest grab and lustily shake the foster parent's wing.

17TH DAY: Chick "feigned death" when Skead looked into the nest; possibly this was the first fear reaction. It had the feathers out of the quills on the flanks and abdomen, but not on the occiput and nape.

20TH DAY: The stump on the tip of the mandible (last seen on the 16th day) was no longer present, and the tip of the lower bill was now perfect in form. The bird's eyes were open fully, circular, the lids kept open regularly. Length of longest primaries 36 mm.; tail 15 mm. The nestling showed a decided dislike at being lightly grasped with the fingers at any point, squeaking, squealing, biting the hand and fingers, and flinching away in jerky moves.

21ST DAY: The honey-guide again was tested for reaction by placing a starling nestling alongside it in the nest, but this evoked no response of any kind from the parasite. The latter showed dislike at being handled, but less vigorously than on the day before.

22ND DAY: Chick still maintained continuous calling, but stopped when inspected; bill pinkish (Skead).

23RD DAY: Bill had a deposit of dark pigment and was becoming dusky ("thin, anaemic black," Ranger).

25TH DAY: Chick well feathered, gray below, light and brown above (paler than in the adult), outer rectrices white (Skead).

26TH DAY: Bill as on 23rd day, nostrils very prominent. Body well feathered, lower abdominal and anal areas being only partly exposed. A colored thickening at the corners of the mouth, absent in the young nestling, developed later (in the third week?); at this stage it was cream colored (Ranger). Chick almost as big as adult barbet. Heard making low peeping noise (Skead).

30TH DAY: Abdominal area was still naked; bare skin around eye cream color, similar to that of the thickenings at the gape. The nestling crouched very determinedly at the bottom of the nest and pecked Ranger's fingers when he attempted to seize it. The tubercles studding the heel callosity were becoming flattened (possibly either by use or pressure against the wood), but the heel pad itself had not shrunk. The bird's voice, heard from outside the nest hole, was very low in tone. Skead reports that a 30-day-old chick called gently for long spells but not as continuously as it did earlier.

33RD DAY: Chick was more silent; beak still pale near gape, horn colored at the tip (Skead).

35TH DAY: Ranger came to the nest at 10:25 a. m., and a barbet flew out. Soon after the young honey-guide showed its head, which protruded far enough to enable the bird to look about in all directions from the entrance hole that was in the underside of a much inclined branch. It drew back out of sight, but repeated the peering at the hole and then withdrawing from sight from time to time for the next hour. It did not utter any sound when at the entrance, and its voice was heard only when one of the barbets came with food; loudest immediately after the feeding when it sounded in tone much like the voice of the kite *Milvus*. It was a low utterance, audible only at close range. During the hour that Ranger watched the nest, the adult barbets fed fruit to the young honey-guide, passing the bits of food to it without entering the nest themselves more than to insert their heads. The barbets took turns in bringing food. One remained about 5 yards from the nest, and on the arrival of its mate with food the former would leave and the other would proceed to feed the nestling. When it was finished it would remain nearby until the other barbet returned with more food.

This was the first day Ranger saw the young honey-guide at the nest entrance. There were two or three previous occasions when it was heard to shuffle back down the nest cavity, but not from so far up, the top of the cavity apparently being as yet out of reach of the nestling. Skead likewise found that a nestling lesser honey-guide 35 days old took the food from its foster parents at the entrance to the nest cavity. It made a rolling call when the latter approached with food, and continued this for half a minute after feeding.

Ranger removed the nestling for examination. Its abdomen was still bare; the tail feathers had reached within three-eighths of an inch of their full growth; the bare skin around the eye and the thickenings at the gape were cream color; the bill was darker than 10 days earlier but not yet as dark as in the adult.

37TH DAY: The young honey-guide apparently left the nest in the morning, and the two barbets continued the usual order of successively feeding it as it perched fairly near the nest site. However, Ranger did not actually see the young fledgling. He came to the nest at 10:09 a. m. and saw one barbet near it. The mate arrived in 8 minutes with two yellow *Aberia* fruits in its bill. The first barbet then departed, and the other one went closer toward the nest; the barbets maintained their pattern of one keeping guard after delivering its food and waiting for the other to return before going off itself, but they were going not to the nest but to a point near and above it that unfortunately was hidden from where Ranger was secreted. He heard the subdued calling of the young honey-guide at least twice, however. On coming closer he failed to find it, and the barbet "on guard" flew off. The nest was empty, and the barbets and the honey-guide did not return to the nesting site again.

In corroboration of Ranger's note, Skead's honey-guide emerged on the 38th day. On that day he looked in the nest in the evening and found the two adult barbets but not the young fledgling (which was there the night before). The following day Skead saw the barbets in the bushveld, 300 yards from the nest. Both made the anxious *snaaar* call which they use to denote apprehension when they have young ones. He could not find the young honey-guide, but from the barbets' behavior he had little doubt that it was somewhere nearby.

Skead goes on to say:

> But, as mentioned, the honey-guide did not return to the nest-hole that night as the barbets' own chicks would have done and the next morning I saw the barbets emerge from their hole and fly away in the opposite direction from where I had seen them with their honey-guide the afternoon before. Never again did I see the chick, and the subsequent activities of the barbets gave no hint of their continued interest therein. From this it must be inferred that either

the honey-guide had acquired immediate independence or had fallen to some predator. Its period in the nest had been 38 days against the 33–34 days of barbet chicks.

It may be noted, at this point, that Gilges (1939) found a young lesser (?) honey-guide in a nest of an African hoopoe, *Upupa africana,* together with three eggs of the host and the shrivelled remains of a dead nestling hoopoe. He considers that in this case "complete ejection was impossible; the honey-guide had succeeded, however, in getting rid of the unfortunate nestling by pushing it into one of the corners of the large cavity."

To return to Skead's account of the nestling *I. minor,* we learn that the barbets fed the honey-guide chick the same food they gave to their young—both insect and fruit diet.

> Throughout its stay in the nest the young honey-guide defecated in the nest tunnel. These faeces must have been removed by the barbets at first because the nest was clean after the chick's departure. But through two adventitious holes in the tunnel floor faeces often fell. They contained the hard chitinous parts of insects and also the pips of youngberry fruit which grew in the garden beside the nest-tree. In this respect the honey-guide differed from barbet chicks who reject the hard insect material and pips before swallowing and whose faeces therefore show nothing hard and undigested.
>
> I sent the insect material to Mr. J. Sneyd Taylor, Government Entomologist at Fort Beaufort C. P., who commented that it "seems to consist mainly of beetles of the chafer type, including those bright-coloured ones found on flowers (*Scarabeidae-Melolonthinae*); also one *Cerambycid* (Longicorn). It is curious that although so much of the insects remains, there is little trace of the brightly coloured elytra."

In Cameroons, Bates (1909a, p. 16) noted that a nestling *I. minor conirostris* taken from a nest of *Gymnobucco bonapartei* had been fed on insects and fruit of the "asen" tree, the usual diet of the barbets.

We now can say with certainty that the nestling *Indicator minor* possesses the mandibular and maxillary hooks found in its larger congener, *I. indicator,* and possibly also *I. variegatus.* In the subspecies *conirostris,* however, Chapin (1924, p. 334) suggested years ago that only the usual type of egg-tooth occurs, but this was probably based on an older nestling that had dropped its hooks. The young of this western race of the lesser honey-guide also has the callosities, or heel pads, found in the typical form (and in the greater honey-guide). Bates (1911, p. 503) took a nestling (subspecies *I. minor conirostris*) from a nest of *Pogoniulus bilineata leucolaima* and noted that it had sharp-pointed tubercles on the heels. He also noted that its eye openings seemed very small, and that the rim of the nostrils formed a raised ring, which is not noticeable in preserved, dried specimens. This last feature appears to be characteristic of various species of *Indicator.* Chapin (1939, pp. 544–545) examined another nestling *I. minor conirostris* collected by Bates in the Cameroons and also noted that it had a conspicuous heel pad, bearing rasplike scales similar to those of a young barbet. This chick, of unknown age, was more completely feathered below than above, although its remiges were nearly half grown. The wings showed no reduction of the inner primaries as found in some species of woodpeckers. The bird no longer had any sign of an egg-tooth or of manibular hooks.

The Postnestling Stage

I have never seen a fledgling *Indicator minor* in the field, and it is astonishing how many observers with many years of field experience have similarly never met with one. Skead's account of the prolonged nest life of a lesser honey-guide, quoted in the previous section of this report, ends with the statement that after it left the nest he never saw it again, although the foster parents did stay around in his garden, and their subsequent activities showed no sign of any interest in their pseudo-offspring. Skead suggests, from this, that either the young honey-guide had become immediately self-sufficient or had met with some disaster. The former is not likely in view of what we know in the related greater honey-guide.

Pringle writes me, from memory, that he has seen young lesser honey-guides with pied barbets "until about two weeks after leaving the nest," but, unfortunately, he was unable to provide any detailed notes. This raises a question on which we have as yet no evidence. It is known that recently fledged young barbets return to the nest for sleeping as do their parents; whether young (or adult) honey-guides also sleep in nest holes or merely perch for the night in the denser part of the branches and foliage of trees is not known. But, if young honey-guides do not return to the nest holes as do barbets, it would seem to follow that this discrepancy in their habits is not necessarily critical for the relations between the parasite and its foster parent. Priest (1936, p. 99) observed a young honey-guide, presumed to be *minor* (and this presumption may be accepted in view of the fact that juvenal *I. indicator* have noticeably yellow throats), not long out of the nest, in his garden where it was fed for four or five days by its foster parents, a pair of Mashonaland gray tits (*Parus afer parvirostris*). From his brief account we get the impression that the fledgling honey-guide was incessantly noisy, giving a repetitive series of *chirri-chirri* notes, and acted as if insatiable as far as food was concerned, like most young altricial birds.

Nothing is known as to whether the full-grown young birds ever form loose, small flocks. In the related *I. indicator* (where the young are identifiable from their plumage) such loose, small aggregations are not unknown.

Food and Feeding Habits

Stomach contents of many adult lesser honey-guides collected by numerous observers reveal quantities of beeswax, insect remains, and often a sticky mass of what probably is honey. Following are a few sample statements from the literature.

Chapin (1939, pp. 541–543) writes that a male from Beni, eastern Congo (subspecies *riggenbachi*) had its stomach filled with bits of beeswax mingled with fragments of chitinous insect parts, probably not from bees. Of *I. minor conirostris* he notes (ibid, pp. 544–545) that the food remains in two examples taken at Lukolela contained beeswax and bits of unidentified insect remains. Farther to the northwest, Bates (1934, p. 237) records only wax in the gizzard of a specimen of *I. minor senegalensis* from near Mopti, French Sudan. Gurney (1860, p. 205) reports that a bird from Natal (*I. minor minor*) had its gizzard full of caterpillars, an observation that is unique as far as I know.

Bates (in Bannerman, 1933, pp. 413–415) found wax and pollen and bits of insects, bees (?) or ants (?), in the gizzards of specimens of *I. minor conirostris* in the Cameroons. He first met with the species in a plantation clearing in the forest at Efulen, where the birds had gathered to feed on bits of bee comb that had been scattered on the ground by the falling of a tree. His native assistants set snares over the pieces of comb and caught several of the honey-guides in this way. In Spanish Guinea, Sabater (in litt. to J. P. Chapin) also trapped two of the birds in a snare baited with bee comb. Of the subspecies *I. minor pallidus* in Nigeria, Marchant (1950, p. 25) states that the stomach contents of three specimens "were a sticky compact yellow mass probably of bees' wax, in one case with hymenopteran remains." He records (1951, p. 73) *I. minor conirostris* feeding on "what looked like small bees or 'sweat flies' " at Owerri, Nigeria. In Kenya Colony, Williams writes me that all the stomachs of a considerable number of specimens collected have held beeswax, white or yellowish in color, mixed with varying amounts of blackish insect particles. The gizzard of one bird (*I. m. minor*) collected in Nyasaland by Benson (1942, p. 300) contained small ants.

I have often watched lesser honey-guides feeding like flycatchers in midair over a woodland pool in the Umtaleni Valley in eastern Cape Province. Ranger's long experience with the birds in this area leads him to think the species gets a good percentage of its food in this way, hawking after May flies and other insects that are common over water. The birds seemed to do their feeding chiefly early in the morning, i. e., for the first hour or more after sunrise, and again in the late afternoon for the two hours before dark. Even during the middle of the day, a bird giving its song-call from a call site occasionally would fly out after a passing insect and then return to its perch. In their feeding flights these honey-guides dart about on erratic courses precisely like flycatchers, and rest for only very brief intervals between these sallies. That this feeding habit is not peculiar to South Africa is attested by the fact that, in northern Tanganyika Territory, Williams collected a male which, when first seen, was flying about like a flycatcher, catching May flies which were coming up in swarms from the river below. It had May flies in its mouth when shot.

Recently Irwin (1953, p. 41) watched some of these honey-guides feeding in Mashonaland, and noted that a "great part of their activity was concentrated on minutely searching the lichen-covered branches; they were very dexterous in clinging to the vertical branches and even clinging upside down. . . . On several occasions one would dart out and snap up a flying insect like a flycatcher." This interest in lichen-covered branches is of interest in view of the fact that the species of thin-billed honey-guides (genus *Prodotiscus*) feed largely on scale insects, which often are found in such situations.

Several observers have written that the lesser honey-guide often perches near a beehive and catches the bees as they go by. Atmore (in Layard, 1875–1884, pp. 169–171) tells of seeing one of these birds at a beehive "as busy as possible catching bees. After watching him for some time, Tom shot him, and his gizzard was full of bees' legs, with the wax on them."

Pringle (in litt.) informs me that at Bedford, Cape Province, he has seen *I. minor* at the entrance of a hive picking up bees (that have died, perhaps), and has also seen it catching live bees as they leave the hive. Not very far away, at "Gameston," near Grahamstown, Skead (1951, pp. 55–56) made the following notes:

> The occasional visitors to the garden always flew to the bee-hives, settled at the entrance for a moment or two and then flew away. At the time the two birds were together, there were several honeycombs protruding from the hives. These were empty except for a few well-developed grubs in some of the cells. I removed a few of the combs and tied them to the branches of a tree where I could observe the birds' actions more easily. At first both approached the combs with the utmost caution, fluttering "nervously" above them or springing up in fright on touching them. However, they soon gained confidence and fed hungrily. One bird began eating at 2:58 p. m. and fed unceasingly until 3:22 p. m. (24 minutes). It then flew to another tree but three minutes later returned to its comb and fed for another 20 minutes, making a total feeding period of 44 minutes. The other bird fed at its comb for only 10 minutes. They ate pure wax, which they "nibbled" from the edges of the combs, and ignored the grubs in the cells. A day or two later I noticed that the grubs had disappeared but these may have been taken by other birds, perhaps Fork-tailed Drongos, *Bhuchanga adsimilis*. Although dead bees always lay scattered near the hives I saw nothing to indicate that the honeyguides fed on them. The numbers of dead bees never seemed to

> diminish when the birds were about; nor did I ever see the honeyguides hawking live bees near the hives.
>
> After a few days' feeding at the combs, the birds, normally timid, became much bolder and often entered an old box lying near the house steps, which contained the remains of wax from another hive. They also came to the bird-bath to drink but I never saw them bathe.

As discussed under the section on cerophagy, this species is a regular wax-eater, and it was on two individuals of this species that Ranger made his experiments showing that the birds are able to digest and assimilate beeswax. All that need be repeated here is that the two birds were kept in captivity on a diet of nothing but clean, empty, dried wild bee comb and water. One of them lived for 25 days, the other a week longer. The latter bird was quite emaciated at the time of death, the former not noticably so. It is not surprising that wax alone is not a sufficient diet as the birds normally consume quantities of insects as well, but the fact that they were able to survive so long on a diet so largely of wax (plus impurities) indicates that this substance is a source of nourishment and that the birds can make use of it.

I once put a piece of bee comb containing some larvae and honey in a branch of a favorite call site of a lesser honey-guide, but although I watched at close range from a blind for several hours on each of three days I never saw the bird come to it. It may have been frightened away from it as the blind was not entirely closed and the bird may have been aware of my presence. However, on coming to the tree each morning I examined the comb and found evidence of some nibbling, but I cannot say that this was done by the honey-guide. The greater honey-guide, in contrast, nibbled at a similar piece of comb placed in its call tree while I remained, unconcealed, only 25 feet away.

At King William's Town, Cape Province, Skead and I once watched a lesser honey-guide which was working its way about in a berry-bearing bush (*Scutia myrtina*, locally known in Afrikaans as "droog-my-keel") apparently looking for food, gleaning one branch after the other. This bird was not actually seen to swallow a berry, but it gave the impression of feeding in the bush, probably on insects. Skead informs me that the berries of this plant are a favorite food of several species of barbets.

A remarkable statement is made by Atmore (in Layard, loc. cit., p. 170): "I can tell you that *I. minor* kills and eats small birds as savagely as *Lanius collaris!* The very first I shot was in the act of eating a sparrow that I saw him kill in flight." The Woodwards (1899, p. 168) state that the lesser honey-guide is a very pugnacious bird and that they have "often seen it hunting the other small birds." That it is pugnacious is further attested by Ranger, who informs me that he has known it to drive off shrikes and other birds larger than itself. In Ethiopia, Blanford (1870, p. 307) saw one pursuing and fighting with a woodpecker. He once saw two lesser honey-guides harassing a fiscal shrike (*Lanius collaris*), giving it a rough time and causing it to fly off screeching in apparent terror. In Tanganyika Territory, Whybrow (in litt.) found that the lesser honey-guide would come to a birdbath in his garden but would neither drink nor bathe; it would merely drive off other birds.

As far as I know, no one has seen a lesser honey-guide eating birds' eggs, a feeding habit known to occur in some parasitic birds.

The almost invariable presence of beeswax in the stomachs of these birds is in agreement with what is known of other species of *Indicator*, but inasmuch as *I. minor* does not guide it must be able to get the wax by itself. Ranger has seen lesser, greater, and scaly-throated honey-guides entering and feeding on wild bees' nests in the eastern Cape Province. Skead's description, quoted above, also reveals that exposed wax is available to these birds.

The food of the nestling lesser honey-guide is discussed in our account of the nest life and development of the young, and need not be repeated here.

Guiding

There is much uncertainty and difference of opinion in the literature as to whether *Indicator minor* guides to bees' nests as do its larger congeners, *I. indicator* and *I. variegatus*. The overwhelming majority of experienced observers agree that the lesser honey-guide does not guide, or, at least, have never found any evidence of its doing so. Among these, the names of the following come to mind (and the list could be extended): Bates, Belcher, Benson, Chapin, Emin, Friedmann, Heuglin, Jackson, Lynes, Moreau, Pitman, Plowes, Potter, Ranger, Rüppell, Serle, Skead, van Someren, Vincent, and Williams. Some of them go so far as to say that the records in the literature of guiding by the lesser honey-guide are all based on misidentifications and that the observations really refer to *Indicator indicator*. That this conclusion is justified seems clear in the instances described by the Woodwards (1899, p. 222), Kirk (1864, pp. 327–328), Lovat (quoted by Ogilvie-Grant, 1900, p. 306), Marshall (1900, p. 251), and W. W. Roberts (1925, p. 43), and these "cases" may be dismissed from consideration.

On the other hand, there are a smaller number of observers who have placed on record observations that cannot be so easily dismissed, and they deserve our consideration.

Swynnerton, who knew his birds well, and who published notes on *I. indicator* (even dividing it, as was then current practice, into *I. major* and *I. sparrmani*) and *I. variegatus*, as well as *I. minor*, wrote (1908, p. 412) from Gazaland, eastern Southern Rhodesia that "as it still appears to be doubtful whether these birds really do lead to honey, I may mention that on May 29th, 1898, I myself and one of my natives were guided by a Lesser Honey-Guide to a bees' nest in a hole in the ground."

Austin Roberts (1911, pp. 73–74), who did know the various honey-guides, found at Boror, Portuguese East Africa, that the lesser honey-guide was much in evidence "whenever chopping trees was undertaken by natives, and then it always sought to lead them to bees' nests." Roberts clung to this statement, refusing to believe that he could have mistakenly recorded data on *I. indicator* under the name of *I. minor*, and repeatedly told me so when I was in the field with him in 1924, and disagreed with Godfrey (1925, p. 34), who stated that the greater and the scaly-throated honey-guide both guide, but "who can produce conclusive evidence for the same trait in the Lesser Honey-Guide?"

According to Chapin (1939, p. 543, footnote), Mr. D. Townley informed him that he had witnessed guiding behavior by *Indicator minor* on two occasions during some 12 years sojourn in Southern Rhodesia. Unfortunately no details are given.

Of those claiming that the lesser honey-guide does guide, Swynnerton, Roberts, and Townley are the only observers with sufficient experience and knowledge to make their notes worthy of serious consideration. I would hesitate to discard their statements were it not for an observation I made near Taveta, Kenya Colony, on March 28, 1925. On that occasion I saw a lesser honey-guide in a tree near me but almost immediately it flew off to another tree some 30 feet away. I followed it and it flew off to still another tree in which were hanging some native-made hives. It stayed in this tree until I came near and then it flew off and did not return. After about a quarter of an hour of waiting I realized the bird was simply gone. The action of the bird did not seem at all purposeful and if I had not been alert to the possibility of guiding behavior it would not have occurred to me to think of it as anything other than the way in which so many birds fly from one tree to another when an observer comes too close to them. Looking back on this experience many years later I cannot help but think that it was purely a coincidence that some native beehives were hanging in the tree to which the bird went, and that it was not really a case of guiding at all. The fact that this coincidence gave it a semblance of guiding makes me wonder if possibly Swynnerton and Roberts may not have had a somewhat similar experience, which they assumed was indicative of guiding behavior. To be taken as indicating guiding behavior, the bird should change its activities when arriving at a bees' nest; should do more than happen to fly to the vicinity of one. I therefore conclude that until further and more detailed evidence is produced we cannot say that guiding has been demonstrated in the lesser honey-guide, a conclusion in keeping with the large amount of negative evidence of almost all other observers.

Miscellaneous Behavior

Pugnacity: As we have already noted in the discussion of its feeding habits, the lesser honey-guide is known to attack and drive off other birds, and has even been reported to kill and eat some of them. This pugnacity sometimes occurs between individuals of its own species, although I know of no case in which one of the birds killed another. When Ranger and Skead put two live female lesser honey-guides in a cage together, they immediately began to fight. One morning, at Umtaleni Valley, Skead witnessed a vigorous chasing about by two birds at the edge of a wooded kloof. Then for two minutes there was silence and then the chase recurred with the birds at times only a foot apart, weaving in and out among the trees. This chasing was accompanied by a series of husky squeaks, *kisk, kisk, kisk.* This went on for about four or five minutes and then Skead saw a bird, apparently one of these two individuals, fly up to the favorite call site and start calling. (From this last action it would seem that this individual was a male.) Five minutes later the bird was at the secondary call site, and, on going closer to watch it better, Skead saw two lesser honey-guides leave; thus, there were two birds there. The puzzling point in all this is that the two birds were amicable at the call site so soon after the violent chasing about that had taken place about 30 yards from that tree.

It may be recalled that A. Roberts (1911, pp. 73–74) mentions that these birds are "very pugnacious and jealous of other members of their own species straying into their own particular hunting grounds." However, on the contrary, we must also remember that, as described in our discussion of courtship behavior, Williams once saw about a dozen of these birds together in one tree, without any sign of fighting.

Sleeping and perching: When Ranger and Skead had two lesser honey-guides in a cage, they once flashed an electric torch on them at night and found them asleep with their bills tucked under the wings. The light did not waken them. On another occasion, during the dawn chorus (4 to 4:30 a. m.), they found the caged birds already awake but perched in a hunched-up attitude and seemingly very lethargic.

Skead and Ranger also noticed that the trapped lesser honey-guides have a habit of swivelling forward and downwards on the perch, releasing their foothold only when they are almost upside down. One of them habitually swivelled right around and regained its old position with a little fluttering of the wings without actually releasing its foothold at all. Once it was seen to do four such rotations in succession.

Enemies: Although no one seems to have recorded finding remains of this species in the gizzard of any bird of prey, I was told once of a pursuit of one of these honey-guides by a lizard buzzard (*Kaupifalco monogrammicus*) in Natal, but the outcome of this incident was not observed.

Ranger once found a lesser honey-guide that had been stung to death by bees. The bird was in a trap near the bees' nest. Ranger recovered over 60 stings from the bird, chiefly from the head and neck.

Description

Indicator minor minor

Adult male: Forehead, crown, occiput, and nape citrine drab to grayish olive, a subocular line from the posterior end of the eye to the sides of the base of the culmen white; interscapulars and feathers of upper back deep olive to dark grayish olive, edged with light yellowish olive, upper wing-coverts, scapulars, and remiges dark grayish olive to chaetura drab, edged with olive-ochre to aniline yellow, the external margins of this color on the secondaries, greater, and median upper wing-coverts very broad, those on the primaries and the lesser upper wing-coverts narrower; remiges internally edged (not terminally) with whitish; feathers of back, lower back, rump, and upper tail-coverts dusky chaetura drab broadly edged and, more narrowly, tipped with olive-ochre to aniline yellow; median two pairs of rectrices fuscous black, internally edged with grayish, and externally very narrowly edged with aniline yellow; the next pair blackish basally (for a longer distance on the inner than on the outer web), then largely white, but broadly tipped with dark olive brown; the outer three pairs white tipped broadly with dark olive brown, this color extending backwards along the outer edge of the feathers for a short distance; cheek and auriculars light grayish olive, a malar band, from the corner of the mouth backwards diagonally, of dark grayish olive; chin and upper throat pale olive gray deepening quickly to deep olive gray on lower throat; breast and sides grayish olive; sides and flanks similar but paler; middle of abdomen, vent, and under tail-coverts white with a pale grayish creamy wash; under wing-coverts whitish washed with pale grayish cream; iris very dark brown; skin around eyes gray; feet pale olive gray; bill black, the extreme basal portion narrowly pinkish white. Measurements in millimeters: wing 88–95; tail 53.5–65.5, culmen from base 10.5–11.8, tarsus 11.5–13.5. Weight, 24.5 grams.

Adult female: Similar to the male but smaller, and with the subocular line to the laterobasal end of the culmen less clear whitish, and the dusky malar stripe averaging less distinct from the surrounding areas. Measurements in millimeters: wing 84–90, tail 52–61.5, culmen from base 10–11.5, tarsus 11–13.

Juvenal (sexes alike): Similar to the adults, but with the subocular line and the malar stripe very slightly developed, if at all; with the lower throat and the breast duskier—hair brown with an olivaceous tinge—and with the rectrices narrower and more pointed terminally, their dusky terminal markings less extensive.

Natal down: None.

Using the above as a standard of comparison, the differences found in the several races of this honey-guide are as follows:

I. minor senegalensis: Paler beneath, the chin white; throat, breast, and sides of abdomen nearly white; lower abdomen and under tail-coverts white; top of head and nape more grayish. Measurements in millimeters, male: wing 85–89.5, tail 56, culmen 11.

I. minor pallidus: "Compared with the nominate race, the whole of the underparts is much paler grey and shows a very slight buff wash; as compared with *I. c. ussheri* Sharpe, the underparts lack the strong olive-yellow wash of that race and the ground colour is distinctly grey, not grey-brown. The crown and nape are also a paler grey than in the nominate race; the grey tone extends further onto the mantle. The olive-golden edging to the feathers of the upperparts is perhaps a trifle paler than in the other races" (Marchant, 1950); bill black, iris brown; feet gray. Measurements in millimeters, female: wing 81.5–84, tail 49–53, culmen 10–11, tarsus 13.

I. m. alexanderi: Similar to *I. m. senegalensis* but with underparts less pure whitish—smoke gray becoming white on chin, lower abdomen, and under tail-coverts. Measurements in millimeters: male: wing 88–95, tail 50–61, culmen 9–10, tarsus 13–14; female: wing 82–86, tail 47–53, culmen 8–9, tarsus 13–14. (I have not seen enough material of *alexanderi, pallidus,* and *senegalensis* to determine whether they are all constantly different enough to warrant recognition, but for the present I accept them on the strength of Bannerman and other writers on West African birds.)

I. m. ussheri: Entire crown strongly washed with golden olive, the entire underparts pale gray-brown with an olive yellow wash; lores blackish. Measurements in millimeters: male: wing 91–92, tail, 58–61, culmen 10, tarsus 14–15; female: wing 83–85, tail 47.5–49, culmen 10.5–12.5; tarsus 16.

I. m. conirostris: The darkest below, and the most contrastingly streaked above, of all the races; chin, throat, abdomen, sides and flanks deep grayish olive; chin in some specimens, but otherwise only the posterior part of the abdomen and the under tail-coverts, whitish; above with the centers of the feathers darker making the streaking more conspicuous, these centers being chaetura drab, even on the crown and occiput; under wing-coverts silvery gray; iris dark brown, bill dark horn color; feet bluish gray. Measurements in millimeters: male: wing 81–96, tail 53–62, culmen 10–12.5, tarsus 15–16; female: wing 79–93.5, tail 50–58.5, culmen 9–10.5, tarsus 13–14.

Specimens from Kavirondo average larger than birds from the Cameroons, as may be seen from the following measurements in millimeters: male: wing 81–91 (Cameroons), 91–93 (Kavirondo); tail 54–57 (Cameroons), 55–59 (Kavirondo). Two examples from Beni, eastern Belgian Congo, are difficult to place as to subspecies; they are either *conirostris* or *riggenbachi*, probably the former. They are immature birds, and if they are *conirostris* they suggest that in this race the juvenal plumage is paler, not darker, below than are the adults.

I. m. riggenbachi: Similar to *I. m. alexenderi* in all respects except darker, the breast darker gray and the edges of the feathers of the upperparts more golden; in the ventral darkness this race helps to bridge the gap between the paler forms and the still darker *conirostris;* iris dark brown; bill blackish, the base of the mandible gray; feet greenish. Measurements in millimeters: wing, male, 89–91; wing, female, 80.5–87.

This race becomes darker, approaching *conirostris*, in the eastern Belgian Congo—from the eastern edge of the Ituri forest south to the eastern base of Ruwenzori.

I. m. diadematus: Similar to the nominate race but darker below, and also on the upperparts where the edgings of the feathers are more dark greenish, less yellowish green; similar to *I. m. riggenbachi* in the dark ventral coloration, but not nearly so golden yellowish above. Measurements in millimeters: male: wing 83–94, tail 53–62, culmen 10–11, tarsus 11.5–13; female: wing 83–87, tail 50.5–51, culmen 9.5, tarsus 11.5–12.5.

I. m. damarensis: Differs from the nominate race in having the top of the head grayer, the chin and throat grayish, the malar stripe absent,[51] and in being smaller in size. Measurements in millimeters, female: wing 81–83, tail 54–57, culmen 9.5–10.5, tarsus 13–13.5.

In studying the geographic variations of this honey-guide, over 400 specimens were examined at different times and with varying opportunity for detailed study and comparison. From this material, especially ample from the eastern and southern parts of Africa, it was concluded that *teitensis* and *albigularis* were not separable from *minor* and that *erlangeri* was probably better treated also as a synonym of

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[51] This character needs verification as Roberts had only females of *damarensis* when he described this race, and females of all the races tend to have the malar stripe poorly developed, if at all.

minor, although in this case the material was not sufficient for as definite a decision as might have been desired. The forms of *conirostris* and of *minor* are considered to be conspecific.

NATIVE NAMES

The following names have been gathered during perusal of the literature. The list undoubtedly is subject to extensive additions.

Native name	*Tribe*	*Locality*	*Native name*	*Tribe*	*Locality*
Dan zuma	Hausa	Northern Nigeria	Sazu	Sofala	Mozambique
Gunda	Hausa	Northern Nigeria	Sequi	———	Angola
Malé	Bulu	Cameroons	Shezu	Chindao	Angola
Ndhlava	Zulu	Natal	Sole	———	Angola
Ndlalala	Singuni	South Africa			

Least Honey-Guide

Indicator exilis (Cassin)[52]

FIGURES 1, 2,e, 3,c; PLATE 21

DISTRIBUTION

This is the smallest of the species of the genus *Indicator*, and is comparable in size to the two species of *Prodotiscus*. It is one of the least well known of African honey-guides in spite of the fact that it has a very extensive range in the equatorial portions of the continent. In tropical Africa it occurs from Portuguese Guinea, Sierra Leone, Gold Coast, Togoland, Nigeria, Fernando Po, Cameroons, Spanish Guinea, the Belgian Congo, Gaboon, and Angola (Chitau, Ebanga, Tyihumbwe), eastwards to French Equatorial Africa (Oubangi-Shari), the southeastern Anglo-Egyptian Sudan (Tembura, Wau, Bahr-el-Ghazal, Bongo, Upper Nile), Uganda, Ruanda (probably), Kenya Colony (chiefly in the western part—Kakamega, southern Guaso Nyero, Sotik, and Mau—but also east to Taveta, and northwards to Kacheliba, near the border of Turkanaland), Tanganyika Territory (recorded, so far, only from the northeastern part—Usambara Mountains and the vestiges of coastal forest at Moa), Northern Rhodesia (Mwinilunga district, Kabompo River, Fort Jameson), Nyasaland (Cholo and Ndirande Mountains, Mlanje), and Portuguese East Africa (near Zobue, Kirk Mountains, near the Nyasaland border). There are some statements in the literature to the effect that this species occurs northeastwards to Jubaland in southern Somaliland, and even to Ethiopia, but these seem to be based on "*erlangeri*," a form now considered to belong not to this species but to *I. minor*.

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[52] *Melignothes exilis* Cassin, Proc. Acad. Nat. Sci. Philadelphia, vol. 8, p. 157, 1856. (Moonda River, Gaboon.)

Throughout the bulk of this enormous range the least honey-guide appears to be restricted mainly to the forested areas, which means that in the eastern part of its range its distribution is decidedly discontinuous and local. However, in northwestern Kenya Colony (Kacheliba), Granvik (1934, p. 51) found it in the tall acacias in the dry open country. At Magadi, southern Guaso Nyero, Williams obtained a specimen in the thick acacia forest along the river. In the Belgian Congo, Chapin records it as not uncommon in the heavy forests of the Upper and Lower Congo, and also in adjacent gallery forests. It is essentially a bird of the lowlands but has been taken as high as 6,900 feet on the western slope of Ruwenzori. Bannerman (1933, p. 415) writes that while *exilis* is a forest dweller at times it ranges some distance north of the forest proper, as was first discovered by Bates in his work in the highlands of western Cameroons. The ranges of the eight races of the least honey-guide follow.

I. e. ansorgei: [53] Known only from Portuguese Guinea (Gunnal).

I. e. leona: [54] Sierra Leone, where known only from Freetown.

I. e. willcocksi: [55] Gold Coast (Prahou, and Mampong, Ashanti district) and Togoland.

I. e. hutsoni: [56] Northern Nigeria (Tatara, Benue Province) to northern Cameroons (Rei Buba).

I. e. poensis: [57] Restricted to the island of Fernando Po, Gulf of Guinea (Bakaki, Basoala, Basepu).

I. e. exilis: Southern Nigeria (Degama), southern Cameroons (Efulen, Lolodorf, Sangmelima, River Ja, Nun River, Donenking, Kumba), Spanish Guinea, and Gaboon (Moonda River, Camma River, Loango, Oyem), eastward in the Belgian Congo from Landana and Chinchoxo (just outside the political area of the Congo itself, in Cabinda) and Eala, to the Ituri River, Avakubi, Irumu, the Semliki Valley, Kartoushi, the western base of Ruwenzori, Idjwe Island, and the highland forest northwest of Lake Tanganyika, Moera, Ukaika, and southward to the Luluabourg area in the Kasai. In the extreme eastern Belgian Congo, present data are a little unclear as typical

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[53] *Indicator exilis ansorgei* Grant, Bull. Brit. Ornith. Club, vol. 35, p. 100, 1915. (Gunnal, Portuguese Guinea.)

[54] *Indicator exilis leona* Grant, Bull. Brit. Ornith. Club, vol. 35, p. 100, 1915. (Sierra Leone.)

[55] *Indicator willcocksi* Alexander, Bull. Brit. Ornith. Club, vol. 12, p. 11, 1901. (Prahou, Gold Coast.)

[56] *Indicator hutsoni* Bannerman, Bull. Brit. Ornith. Club, vol. 49, p. 20, 1928. (Tatara, Benue Province, Nigeria.)

[57] *Indicator poensis* Alexander, Bull. Brit. Ornith. Club, vol. 13, p. 33, 1903. (Bakaki, Fernando Po.)

exilis is recorded from Idjwe Island in Lake Kivu, while a specimen identified as *pachyrhynchus* has been taken at Mulungu in the highlands west of that lake.

I. e. pachyrhynchus: [58] The Bahr-el-Ghazal and Upper Nile areas of the Anglo-Egyptian Sudan (Bongo, Wau, Tembura), southeastwards across Uganda (Mabira forest, Kakamari, Luankuba forest in Ankole, Lugalambo, Lake Victoria) to northwestern Tanganyika Territory (Bukoba), probably to Ruanda, to the highlands west of Lake Edward and Lake Kivu, Belgian Congo (Mulungu, Lutunguru, Dundazi, Tshibinda), and to the western part of Kenya Colony (Sotik, 7,500 feet, and Kakamega to Mau forest), and to northwestern Northern Rhodesia (Kansoku, lat. 12°22′ S., long. 24°05′ E.) (apparently skirting eastwards and southwards around the range of *exilis!*).

I. e. meliphilus: [59] The Elgon area of extreme eastern Uganda (Mount Moroto, Soronko River) and Kenya Colony from Turkanaland (Kacheliba) and the drier, lower parts of the Suk area, east to Taveta, south in suitable spots in Tanganyika Territory (Moa near Amani, western Usambara Mountains, Kidugallo (between Morogoro and Dar-es-Salaam)), Nyasaland (Cholo, Ndirande, Mlanje), Mozambique (near Zobué, Kirk Mountains), Northern Rhodesia (Mwinilunga, Kabompo River, Fort Jameson), and Angola (Chitau, Tyehumbwe, Ebanga, and Quibula near Benguella). In areas such as western Kenya Colony and Northern Rhodesia where *meliphilus* and *pachyrhynchus* approach each other, the latter is probably in the patches of evergreen forests while the former is in the more open acacia woodlands. Also, it seems, from specimens examined, that *meliphilus* is an unusually distinct race, showing no tendency to intergrade with *pachyrhynchus* or *exilis*. No true intermediates appear to be known. If Verheyen (1953, pp. 406–407) is correct in recording both *exilis* and "*angolensis*" (= *meliphilus*) from the Upemba Park, and if the two occur together side by side all the way from Lake Upemba to the Mwinilunga District of Northern Rhodesia, it would seem necessary to give *meliphilus* full specific status. For the time being it is not possible to state that the two have been recorded from the same area in the Upemba Park, but the possibility of *meliphilus* being a species and not a race of *exilis* should be kept in mind.

Breeding Range and Season

Like the other species of honey-guides, *Indicator exilis* is not migratory (as far as we know, which is, admittedly, not much). It might therefore be expected to breed throughout its range, but so few observations are on record that it is not possible to outline seriously its breeding range and season. The available data on localities and dates of evidence of breeding are given below.

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[58] *Melignothes pachyrhynchus* Heuglin, Journ. Ornith., vol. 12, p. 266, 1864. (Bongo, southeastern Sudan.)

[59] *Melignothes exilis meliphilus* Oberholser, Proc. U. S. Nat. Mus., vol. 28, p. 869, 1905. (Taveta, Kenya Colony.)

GOLD COAST: Mampong, Ashanti, February 10, two males collected showing signs of breeding condition (Bannerman, 1951, p. 349; ex W. Lowe, 1937, p. 653). This refers to the subspecies *willcocksi*.

NIGERIA: Near Lagos, January 30, male with enlarged testes collected. Specimen in British Museum (subspecies *hutsoni*).

FERNANDO PO: Basoala, May 9, male with enlarged testes collected.

CAMEROONS: Bitye, January 29, female with developing ovarian eggs, and Efulen, July 11, male with enlarged testes, both collected by Bates; River Ja, March 22, fledged juvenal bird taken by Bates (Sharpe, 1907, p. 440) (subspecies *exilis*).

BELGIAN CONGO: Irumu, Ituri forest, October 16, female "evidently breeding" (Ogilvie-Grant, 1910, p. 415); East Congo forest, October 16, female in breeding condition (British Museum); Iyonda, near Coquilhatville, June 7, female with egg in oviduct (subspecies *exilis*); Upemba Park, June, two males with enlarged testes.

SPANISH GUINEA: "Around September,"egg laid by trapped bird (subspecies *exilis*).

UGANDA: Mount Elgon, July, nestling found in nest of *Pogoniulus b. jacksoni* (subspecies *meliphilus*).

KENYA COLONY: Sotik, October 5, female with fully formed egg (Sharpe, 1892, p. 309) (subspecies *pachyrhynchus*).

TANGANYIKA TERRITORY: Morogoro district, February 21, male with very large gonads.

NYASALAND: Cholo Mountain, September 3, female, almost ready to breed; Ndirande Mountain, Blantyre, September 2, male with testes somewhat enlarged (subspecies *meliphilus*).

SONGS AND CALLS

Bates and others have written that this little honey-guide is generally silent, but Bates, in the Cameroons, did once hear it utter a repetitive monosyllabic note, *kwiew, kwiew, kwiew,* a description that recalls somewhat the "song" of *Indicator minor*.

Chapin (1939, p. 540) heard a short, dry trilling note from three of these birds at Avakubi. In the Usambara Mountains, Tanganyika Territory, Moreau (in Sclater and Moreau, 1932, p. 665) heard the subspecies *meliphilus* make a sibilant sound, like that produced by whistling through the teeth. Finally, as noted in our short account of courtship behavior, in Northern Rhodesia *meliphilus* was heard giving a very soft twittering sound.

Courtship and Mating

There are no published data. If one may judge by what is known of the better known species of *Indicator*, the least honey-guide probably is not much given to courtship displays. However, E. L. Button of Lundazi, Northern Rhodesia, writes me that he has seen what seems to be courtship behavior. "The courtship of the least honey-guide resembles that of the blue flycatcher (*Erannornis albicauda*) to a great extent. The male bird fans his tail and flits about in the vicinity of the female uttering a very soft twittering sound."

Eggs and Egg Laying

Almost nothing is known; the following being the only pertinent observations. At Iyonda, near Coquilhatville, Belgian Congo, on June 7, 1953, Father G. Michielsen took a fully shelled egg from the oviduct of a least honey-guide. It measured 18 by 13 mm., and was pure, unmarked white in color. In Spanish Guinea, early in September 1951, G. Sabater found a least honey-guide in a trap baited with honeycomb, and also found an egg beneath the trap. He sent the bird and the egg to J. P. Chapin, who has kindly written me the following details. The egg, pure white and rather smooth, was fresh, but it was broken by the weight of the birds sent in the same package and was stuck to the paper. Before attempting to remove it from the paper Chapin measured it with calipers and found it to be approximately 17 by 13.5 mm. When he tried to soak the paper in water and free the broken egg, everything went to pieces. He felt, however, that he had the dimensions correct to within about half a millimeter.

There is, unfortunately, an element of uncertainty about this egg. Sabater trapped examples of *Indicator maculatus* and *I. minor conirostris* as well as *I. exilis*, and, in fact, the package he sent to Chapin containing the egg also contained injected specimens of all three species. All he gave as evidence concerning the egg was that he found it beneath the trap but did not say explicitly that it was found when a least honey-guide was in the trap. That it does refer to this species is highly probable. Chapin, who examined it when it was still more or less intact, felt it could only be an egg of *I. e. exilis*.

Hosts or Victims

As far as I have been able to learn, only two nestling least honey-guides have ever been found in nests of their fosterers, and no eggs attributable with any definiteness to this species have yet been found in any nests. Of the two instances of parasitized nests, one only is identified to species. Van Someren (in litt.) informs me that he once collected a juvenal least honey-guide from a nest of a Kenya golden-rumped tinker-bird (*Pogoniulus billineatus jacksoni* (Reichenow)) on Mount Elgon in July. This constitutes the only definite host record. The other honey-guide chick was in an unidentified barbet's nest. In the Cameroons, Bates (1930, p. 267) writes that "for its propagation it seems to depend on the small Barbets, in a hole of one of which was found a young Little Malé, its stomach very full of Barbet's food."

Chapin informs me (in litt.) that at Iyonda, near Coquilhatville, Belgian Congo, on June 7, 1953, Father G. Michielsen shot a female least honey-guide close to a nest of *Pogoniulus subsulphureus*,[60] where the little barbet was on guard. The honey-guide had an egg in its oviduct.

For further possible but wholly indefinite records see the accounts of the barbets of the genus *Pogionulus* discussed among the hosts of *Indicator minor*.

FOOD AND FEEDING HABITS

ADULT: A specimen (*meliphilus*) collected in Kenya Colony by Williams had beeswax and tiny black insect remains in its gizzard. Two specimens from the Belgian Congo (typical *exilis*) contained beeswax, insect remains, and a seed (Chapin, 1939, p. 540). A specimen collected in Spanish Guinea by Sabater had remains of three species of ants, one elaterid beetle, one nitidulid larva, one fly, one feather, and some beeswax in its gizzard. In southeastern Nigeria, Marchant (1953, p. 51) found small black hymenopterous insects in the gizzard of a least honey-guide (subspecies *exilis*).

In order to test the presence of wax in his birds, Chapin placed some of the stomach contents on a knife blade and heated it, whereupon it melted, and solidified again when allowed to cool. In the Cameroons, Bates concluded that the species must depend in part on certain tiny hymenoptera other than bees, but he also found honey in their gizzards. Serle (1950b, p. 366) reported insects in the stomach of a bird shot at Kumba, Cameroons. In the Gold Coast, Alexander (1902, p. 364) frequently observed the least honey-guide (subspecies *willcocksi*) "whenever a swarm of flying ants appeared. It would dart upon them and then retire to its original perch to devour its prey." In Tanganyika Territory, Moreau (Sclater and Moreau, 1932, p. 665) noted fragments of small beetles in the gizzard of one of these birds (race *meliphilus*).

Chapin writes that it is not known how this species "procures its honey-comb; but since it asks no aid of man, I suspect it of having some other mammalian ally."

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[60] This would refer to the subspecies *flavimentum* (Verreaux). *Barbatula flavimentum* Verreaux, Rev. et Mag. Zool., ser. 2, vol. 3, p. 262, 1851 (Gaboon).

In Mozambique, Jack Vincent (1935, p. 13) observed an example of the subspecies *meliphilus* creeping about like a woodpecker on the vertical trunk of an enormous forest tree, and in and out of a narrow crack in it. In Nigeria, Hutson (in Hutson and Bannerman, 1931, p. 201) noted a bird (subspecies *hutsoni*) busy in the foliage of a thickly leaved tree. While in neither of these cases is it stated that the bird was foraging for food, that would seem to be the implication.

Specimens caught by Sabater in Spanish Guinea came to traps baited with honeycomb.

NESTLING: Our knowledge is limited to the bare statement by Bates (1930, p. 267) to the effect that a young least honey-guide found in a small barbet's nest had its stomach filled with the kind of food that the barbets give their own young.

DESCRIPTION

Indicator exilis exilis

ADULT MALE: Almost exactly a miniature version of *Indicator minor conirostris* in coloration except on the underparts, which are paler in *exilis;* middle of forehead and a line from there to the anterior angle of the eye olive blackish; below this line a white loreal patch on either side; rest of forehead, crown, occiput, and nape deep olive to dark olive, the crown, occiput, and nape with an olive green wash; interscapulars, scapulars, upper wing-coverts, feathers of the back and rump, and the upper tail-coverts deep olive to dark olive, conspicuously edged with olive ochre, making a strikingly streaked pattern; remiges very dark olive brown to fuscous, the primaries narrowly and the secondaries broadly edged externally with olive ochre to aniline yellow, the remiges internally edged with whitish; median two pairs of rectrices very dark olive brown to fuscous, slightly paler along the margin of the inner web and narrowly edged with aniline yellow on the outer web; next pair similar but with a fairly extensive area of white, this area more extensive on the inner than on the outer web, but tipped with dark brown; the outer three pairs white tipped broadly with dark olive brown; cheeks and auriculars deep olive to dark olive to olive brownish; chin and upper throat whitish; a malar stripe running from the corner of the mouth diagonally backwards very dark olive to dark chaetura; breast, abdomen, and sides grayish olive, the lower abdomen and under tail-coverts creamy white; feathers of the flanks with broad shaft streaks of dark brownish olive, edged and tipped with creamy white; under wing-coverts creamy white with a varying amount of grayish wash; iris brown; eyelids dark gray; bill brownish black with the base of the mandible light pinkish gray; tarsi and toes dusky grayish green. Measurements in millimeters: wing 70–78, tail 45–51, culmen from base 8–9.8, tarsus 15–16.

Adult female: Similar to the male, but with the white loreal spots and the dusky malar stripe less conspicuous; size somewhat smaller. Measurements in millimeters: wing 65–79; tail 39–49; culmen from the base 8–9.5; tarsus 11–13 mm.

Juvenal: Similar to the adult but less distinctly streaked on the back, more streaked on the crown and occiput; the lores not white but olive like the cheeks, the entire upperparts, head and body, more tinged with greenish, the malar stripes absent or very indistinct (perhaps due partly to the fact that the sides and underparts of the head are generally darker than in the adult); throat, breast, and abdomen duskier and with a more pronounced olive smudge, and the rectrices narrower and noticeably more pointed. A young bird from the Cameroons is said by Sharpe (1907, p. 440) to have the bill reddish brown, the feet pale reddish brown.

Natal down: Unknown, if any.

The plumage characters of the seven subspecies differ from the above as outlined below.

I. exilis ansorgei: Differs from typical *exilis* in having the head paler gray, lacking the olive wash; in having the feathers of the back and the wings less distinctly streaked, their median portions less different from their margins; and in being somewhat larger generally. Measurements in millimeters: male: wing 80, tail 47, culmen 8, tarsus 12.5; female: wing 71, tail 42, culmen 8, tarsus 12.5.

I. exilis leona: Agrees with *I. e. ansorgei* in having the upperparts less streaked than in *I. e. exilis* but is even more uniform oilve on the interscapulars and upper back; on the underparts it is slightly darker, deeper olive brown than *I. e. exilis;* size small. Measurements in millimeters, one male: wing 70, tail 42, culmen 9, tarsus 11.

I. exilis willcocksi: Like *I. e. exilis* but has the whole of the crown and neck greenish, the upperparts more brownish olive, not grayish. Soft parts: iris dark brown, bill black, feet very dark gray. Measurements in millimeters: male: wing 77, tail 51, culmen 8, tarsus 12; female: wing 68, tail 39, culmen 8, tarsus 13.

I. exilis hutsoni: One of the largest of all the subspecies; the upperparts of the body less conspicuously streaked than in the nominate form, and the underparts paler, almost as in *I. e. ansorgei* from which form it is recognizable by the fact that the entire head is olive like the back in *hutsoni,* not grayer than the back as in *ansorgei;* the bill broader and more swollen than in any of the other races. Measurements in millimeters: males: wing 78.2–80.0, tail 50–50, culmen 8.5–9, tarsus 14–14.

I. exilis poensis: Differs from *I. e. exilis* in having the entire head gray, and the general tone of the upperparts of the body slightly paler in tone. Measurements in millimeters: male: wing 74–79, tail 48–50, culmen 8.7–9, tarsus 13.5–14; female: wing 66–72, tail 45, culmen 9, tarsus 12.

A juvenal female resembles the adult but has the feathers of the breast and abdomen transversely obscurely barred with paler and with duskier olive; the rectrices more pointed, with less dusky terminal blotches.

I. exilis pachyrhynchus: Similar to *I. e. exilis*, but larger, slightly darker grayish, less olivaceous, below; occasional specimens have the throat indistinctly streaked with dusky. Measurements in millimeters: male: wing 74.5–82, tail 48–54.1 (one 59.8 from Dundazi, southwestern Lake Kivu), culmen from base 8.5–10, tarsus 13–13.5; female: wing 73.2–74.5, tail 44.5–46.5, culmen from base 8.5–9.5, tarsus 12.

I. exilis meliphilus: Similar to *I. e. exilis*, but much paler below, much less distinctly streaked, more uniform, above, the top of the head more strongly tinged with olive green. In the original description this race is said to be larger than the nominate race, but further material of both forms shows that this is not a constant character. Measurements in millimeters: male: wing 73–79, tail 44–48, culmen from base 8–9, tarsus 12.5–13.5; female: wing 70–76.2, tail 41.2–48.2; culmen from base 7–8.4, tarsus 12.2–12.5. The type specimen, collected by W. L. Abbott, no longer fits the description as the whole anterior part of the head back to the occiput, auriculars, and throat have darkened due to the collector's use of a solution of corrosive sublimate as a preservative on the bill, thereby completely hiding the white loreal spots and reducing the color characters of other parts. For this reason, the description given by Oberholser (Proc. U. S. Nat. Mus., vol. 28, p. 869, 1905), with which fresh material agrees, is a more reliable reference basis than the type itself.

It appears that the supposed race *angolensis* is best treated as the same as *meliphilus*, but further material may demonstrate that the Angola population is slightly larger, especially in wing length, slightly duskier on the back, and with more pronounced dark shaft stripes on the feathers of the flanks than typical East African *meliphilus*.

The colors of the soft parts of an adult female from the southern Guaso Nyiro, Kenya Colony, are recorded as follows: iris dark brown, bill lead gray, base of the lower mandible flesh pink, bare skin around eye lead gray, feet dull blue-gray.

NATIVE NAMES

The Bulu people of the Cameroons call this bird "male"; the Lulega tribe, Lake Kivu, eastern Belgian Congo, call it "semanzuki," while in the Upemba Park, also Belgian Congo, it is called "mpia."

Orange-Rumped Honey-Guide

Indicator xanthonotus Blyth [61]

FIGURES 1, 2,*f*, 3,*d*; PLATES 18, 23

This species is a bird of the Himalayan highlands about whose life history almost nothing has been recorded. It is the most strikingly colored of all the honey guides.

DISTRIBUTION

This honey-guide ranges in the Himalayas from Bannu and Huzara, near the border of Afghanistan and the North-West Frontier Province of India, east to Murree (Abbottabad), Garhwal, Darjeeling, Assam (Naga Hills, Margherita) and to northern Burma (Myitkina District). The population inhabiting the eastern part of the range—northern Assam and northern Burma—has been separated as a distinct race, *fulvus*, which is characterized by being darker, more blackish on the upperparts and underparts of the body, and by having the yellow on the forehead more restricted posteriorly. Ripley (1951, pp. 2–3) found this honey-guide in the Naga Hills near Pfutsero—28 miles east of Kohima at 6,000 feet and on the slopes of Japvo, 10 miles southeast of Kohima, at 7,000 feet. In Garhwal, Koelz collected specimens near cliffs at an altitude of 9,000 feet, and also above tree line in Kumaun. Inasmuch as other naturalists have described the bird as a denizen of heavy forest, it is worthy of note that it may range above the tree line.

In reply to an inquiry on this ecological point, Ripley (in litt.) informs me that the westernmost population of the species occurs in the coniferous and dry deciduous woods of the western Himalayas, which are very open compared with the dense, wet forest patches in which the eastern subspecies, *fulvus*, dwells, while the birds occurring in the central portion of the range do seem to be less rigidly restricted to truly forested areas than do their counterparts farther to the east.

It is possible that the extreme western portion of the species may prove separable from typical *xanthonotus* (described from Darjeeling), in which case Hume's name *radcliffii*,[62] based on a bird from Huzara, would be available for them. Pending study of more material than is available to me at present, the ranges of the two recognized races are as follows.

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[61] *Indicator xanthonotus* Blyth, Journ. Asiatic Soc. Bengal, vol. 11, p. 116, 1842. (Darjeeling.)

[62] *Indicator radcliffii* Hume, Ibis, ser. 2, vol. 6, p. 529, 1870. (Huzara.)

I. x. xanthonotus: From Bannu and Huzara in western Punjab, near the Afghanistan border, east to Murree, Garhwal, Nepal, and Bhutan at elevations of 5,000 to 9,000 feet.

I. x. fulvus: Naga Hills, northern Assam, Margherita, and the Myitkina District, northern Burma, above 5,000 feet.

In Garhwal, Koelz was informed by the natives that the bird does not migrate. However, Ripley (1950, p. 376) considered it to be seasonal at high altitudes in Nepal, being absent in the winter. He saw some old wild bees' nests on open rocky ridges above Dhankuta, and thought the area a suitable place for this honey-guide. Local people informed him that such a bird was present there during the monsoon season.

Breeding

Nothing is known of the eggs, nestlings, or even the fledglings of this honey-guide. We can only wonder if it will be found to be parasitic in its breeding like the other honey-guides, although Baker (1927, p. 132) writes that it "lays its (presumably) white eggs in nest-holes of Woodpeckers and Barbets as the African species do." In Garhwal and Assam, Koelz thought the breeding season began in late May, judging from the condition of the gonads of his specimens.

Songs and Calls

In northern Burma, Smythies (1949, p. 645) heard an occasional single *tweet* note given by a bird sitting motionless in a high branch of a densely foliaged tree.

The only other mention of a vocalism in the literature does not help us much. Magrath (1909, pp. 153–154) writes that "according to Colonel Buchanan it has a peculiar note which he was unable to describe."

Food and Feeding Habits

Although nothing is known as to whether or not this species ever guides humans or other creatures to bees' nests,[63] it does derive a good deal of its nourishment from the hives of wild bees. In Muree, Magrath (1909) watched one of these birds at a hole in a tree feeding on bees which were swarming there. Stuart Baker writes that it feeds on "hymenoptera and possibly other insects." Koelz (in litt. to J. P. Chapin) describes seeing these birds, singly or occasionally two or three at a time, near cliffs in Garhwal. On those cliffs were swarms of bees which built exposed combs of beeswax there. The honey-guides would perch on the trees and then fly to the cliffs where they often clung like woodpeckers and pecked at the wax. Sometimes they would be within a few feet of the bees, of which they seemed wary and afraid. They gave no sign of asking assistance from man. Gizzards of a dozen or so specimens collected all contained beeswax, also remains of craneflies, and, in one instance, a mammalian hair, probably accidentally swallowed. Stoliczka (1873, p. 425) reports six wasps and some green vegetable matter in the gizzard of his specimen taken at Dungagally.

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[63] No credence may be attached to Handley's story of being led to a bees' nest by a "honey-bird" in southern India (Leonard M. H. Handley, Hunter's Moon, p. 218, 1933). No honey-guide is known to occur within a thousand miles of his area, the Blue Hills of Ranga.

The gizzard of Ripley's specimen from Assam (the type specimen of *I. x. fulvus*) was sent to me, and its contents were examined by Dr. E. A. Chapin and myself. It contained a quantity of unidentifiable particles, probably wax, a great many pieces of flies' legs, five heads of undetermined species of ants, a compound dipterous eye, remains of at least three specimens of two species of chrysomelid beetles and one of a hydrophilid beetle, and two shreds of downy feathers. The bits of feathers were probably adventitiously swallowed after preening, or some such activity.

That this species also catches insects on the wing like its African relatives is shown by the notes made in Burma by Smythies (1949), who noticed it "sallying out at intervals and fly-catching in the clumsy manner of a Bulbul . . . I must have watched it for quite half-an-hour before collecting it for identification. It confined its fly-catching to a 50-yard stretch of sunlit stream."

Ripley reports that the local native name in the Naga Hills for this bird is *mephi tsu kelie para*, which is said to mean "the bird that eats bees," a further confirmation of its interest in hives.

The late Austin H. Clark called my attention to a statement by Read (1941, p. 12) that "in the 'Po-wu-chih' of Chang Hua (Chin dynasty) it states that honey and beeswax come from the solitary glens of various mountains in the South. The places where the honey is found are all steep cliffs which cannot be climbed, so people go up to the top of the mountain and are let down the precipitous cliffs in a basket and collect the honey. When the bees go away and leave the wax on the rocks flocks of birds like sparrows come and peck it nearly all away. The birds are called . . . ling ch'ueh . . ." According to Wylie (1902), the "Po-wu-chi" was originally drawn up by Chang Hwa in the latter part of the third century, but his production appears to have been lost during the Sung period and the work as we know it was compiled from extracts of it preserved in other works; the compilation in ten books, under the title "Sûh pô wûh ché," was made by Lé Shih about the middle of the 12th century.

My colleague, Archibald G. Wenley, Director of the Freer Gallery of Art in Washington, has kindly searched the old Chinese literature in my behalf and has translated the following from the "T'ai-ping-yü-lan," a great 80-volume encyclopedic work compiled by Imperial command by Li Fang and his coworkers and completed in 983. This work quotes the third-century account of Chang Hua more fully than does Read, as the following extract shows.

> It also says in many distant countries there are secluded places in the mountain districts which produce beeswax. These beeswax places are all abrupt cliffs and rock walls which are unclimbable, and only by raising baskets to the top of the mountain and lowering them to the bottom is it obtained. When the bees leave not to return, the surplus hives and wax on the rocks are unlimited. There is a bird small in shape as a sparrow. It comes in flocks of thousands to peck at it. By spring all is used up and the place is as if it had been scrubbed and washed. In spring the bees all return to the clean place just as before. Year by year it is like this without any confusion. People also note these smooth places. They call them (the birds) wax honey birds, and call them spiritual sparrows (because) they are entirely unable to catch them.

There can be little doubt that the wax-eating bird is the Himalayan honey-guide; at least it is the only bird in the area known to eat bee comb. The size of the flocks is undoubtedly exaggerated and this discrepancy need not be taken too seriously. It follows that 1,700 years ago the Chinese scholars had heard of the wax-eating habit of a bird they had never seen themselves, a bird that remained unknown to the Western World for nearly 16 centuries longer, and of whose wax-eating habits we have only become aware in the last few years. There is even a curious parallel between the old Chinese appellation "spiritual sparrow" and Humes' subgeneric one, "*Pseudofringilla*," proposed for this bird some 30 years after Blyth first made it known.

Miscellaneous Behavior

Like the common African indicators, this one also sits in an erect attitude, apparently in a shaded perch by preference (Smythies, 1949); its posture is described by Magrath (1909), however, as "very dove like. It sits with head sunk on breast, feathers rather puffed out and wings drooping so as to display the vivid yellow patch down the lower back." This is quite reminiscent of the hunched-up pose assumed by *Indicator variegatus* and *I. maculatus*.

The flight is described as heavy and dipping, "like the larger and more clumsy Barbets" (Baker, 1927).

Magrath records seeing one of these birds bathing in a small stream.

Description

Indicator xanthonotus xanthonotus

Adult male: Forehead, anterior part of crown, chin, and cheeks silky golden yellow; feathers of top and sides of head (aside from cheeks) and back of neck chaetura brown washed and margined with olive-yellow (this color often hiding the dark brown areas), and, on their concealed basal portions, yellowish white; interscapulars fuscous brown, edged with olive green; scapulars, upper wing-coverts, and remiges chaetura drab to fuscous, margined with Naples yellow, these edgings more pronounced on the scapulars and upper wing-coverts, less distinct on the remiges; the secondaries and longer scapulars with a whitish margin on their inner webs; feathers of upper back fuscous edged with olive yellow; median area of lower back and rump bright orange-yellow, the basal portions of the feathers paler, and many of them with a dusky streak or spot; lateral parts of rump and upper tail-coverts blackish, the longer coverts edged with yellowish white; rectrices fuscous black, the outermost pair, which are narrow, pointed, and about 20 mm. shorter than the next pair, tipped with white or grayish white, and with a broad streak of the same extending along the shaft, the next pair (about 8 mm. shorter than the more median ones) similar except that the terminal white area is confined to the inner web, rest of rectrices with no terminal white; throat ashy gray lightly washed with olive yellow; breast ashy gray with an olivaceous tinge, the feathers with fuscous shaft stripes giving a streaky appearance to this area; abdomen, flanks, and under tail-coverts similar but with the shaft stripes so much widened as to practically cover the feathers, which thus appear fuscous to dull earth brown with lateral margins of olivaceous ashy gray; under wing-coverts whitish, somewhat mottled with blackish and washed with yellowish or buffy at the edge of the wing; undersurface of remiges dull earth brown, margined internally with paler; iris dark brown; bare circumocular area very pale green; bill yellow, somewhat dusky terminally; at the base of both the maxilla and the mandible, as well as on the chin, black bristles are present, none present above the large, swollen, triangular nostrils; tarsi and toes pale greenish horny. Measurements in millimeters: wing 92–96; tail 56–61; culmen 8–9; tarsus 13–14. Weight, 29 grams.

Adult female: Similar to the male but slightly duller, the rump patch sulphur yellow, the yellow areas on the forehead, crown, and sides of throat paler and less extensive; whole bird somewhat smaller. Measurements in millimeters: wing 82–92, tail 55, culmen 8.6; tarsus 12.7.

Other plumages are unknown.

From the typical race, described above, the adult male of the Assamese subspecies *I. xanthonotus fulvus*[64] differs as follows: Similar to *I. x. xanthonotus*, but darker, more blackish on the upperparts and on the abdomen, thighs, and under tail-coverts. The streaking of the abdomen, though blackish, is less in extent, thus less prominent. On the forehead the golden patch extends somewhat less far back on the crown, and the edging to the feathers of the back and scapulars is reduced; iris brown, bill yellowish horn distal half of upper mandible and lower mandible brown; feet grayish brown. Measurements in millimeters: male: wing 90, tail 57, culmen 11; female: wing 86, tail 56, culmen 10 (ex Ripley, 1951, pp. 2–3).

Genus *Melichneutes* Reichenow

Melichneutes Reichenow, Ornith. Monatsb., vol. 18, p. 160, 1910. (Type, by monotypy, *Melichneutes sommerfeldi* Reichenow=*Melignomon robustus* Bates.)

Ceriocleptes Chapin, Bull. Amer. Mus. Nat. Hist., vol. 34, pp. 512, 513, 1915. (Type, by monotypy, *Ceriocleptes xenurus* Chapin=*Melignomon robustus* Bates.)

Similar to *Indicator* (subgenus *Indicator*) in its bill, general form, and proportions except for the tail, which is unusually broad basally and is composed of 12 rectrices, the two middle pairs of which are equal in length, somewhat pointed terminally and curved strongly outwards to form a lyrate tail, the next pair considerably shorter, less acutely pointed, and slightly curved outwards; the remaining three pairs are straight, very narrow and stiffened, and become successively shorter so that the outermost pair is less than half as long as the median one; the tail coverts very elongated, the lower ones as long as the longest rectrices and, in the male, projecting into the fork of the tail; body depressed dorsoventrally, the keel of the sternum less well developed than in *Indicator*; oil gland slightly tufted.

This remarkable bird performs very elaborate aerial evolutions,the sound accompaniment to which seems to be produced by the vibration of the outer rectrices, as in some species of snipe.

This genus is not known to guide.

The breeding habits are unknown, but the bird probably is parasitic.

Monotypic; forests of the Lower Guinean region, western and central Africa.

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[64] *Indicator xanthonotus fulvus* Ripley, Postilla, No. 6, p. 2, February 28, 1951. (Pfutsero, eastern Naga Hills, Assam.)

Lyre-Tailed Honey-Guide

Melichneutes robustus (Bates) [65]

FIGURES 1, 2,*g*, 3,*g*, 6; PLATES 19, 23

DISTRIBUTION

This, perhaps the most peculiar of all the members of the family, is a very imperfectly known bird of the primeval rain-forests of tropical West Africa, from the Niger Delta (near Port Harcourt and Umuagwu, near Owerri), Cameroons (Bitye, Efulan, Lolodorf, Sangmalima, Minkang, Yaunde, and Dumé), northern Gaboon (Oyem), and the Congo forest (Medje, Yangambi north of Stanleyville, Ibembo, Buta, Kitenge, Pawa, and Avakubi) east to the Semliki Valley (Tungudu, Mushinene) and to extreme western Uganda (Bwamba forest),[66] south to Kasese, west of Lake Kivu, to the Kasai (Lusambo), and to northwestern Angola (presumably west of the middle Cuanza River). In the course of his very prolonged field work in the Belgian Congo, Chapin obtained but a single example. However, after learning the identification of the distinctive call of the species, he realized that he had heard it many times during several years at Medje, Pawa, and Avakubi. Chapin (1939, p. 555) suggests, therefore, that the bird is probably fairly common but is extremely difficult to observe and collect. The species is, of course, nonmigratory, and has been heard calling in Gaboon in all months except May and in the Congo forest in all except April and May.

GUIDING

There is no evidence of any guiding habit in this species, certainly not as far as humans are concerned. It is true that some years ago Chapin (1924, pp. 334–336) suspected that the curious note given by the bird may summon some mammalian or avian accomplice to aid it in robbing bees' nests, but this is still an unsupported suggestion. It may be noted, as nothing more than a thought, that Rougeot (1950, p. 63) found a peculiar and as yet unexplained attraction the large hornbills have for the parts of the forest frequented by the lyre-tailed honey-guide. He asks if this is merely a coincidence or whether the hornbills may profit, together with other aboreal creatures, from the indications of bees' nests furnished by the honey-guides. As far as I have been able to learn, no honey, beeswax, or bee larvae have been reported from the gizzards of any of these forest hornbills.

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[65] *Melignomon robustus* Bates, Bull. Brit. Ornith. Club, vol. 25, p. 26, 1909. (Bitye, River Ja, Cameroons.)

[66] The occurrence of this honey-guide in the Bwamba forest is based solely on the fact that its distinctive notes have been heard there. It has not been seen or collected there.

Breeding Season

In the northern Belgian Congo the breeding season seems to be from March to September and an undetermined period before and after those months. At Medje, Christy obtained a nestling in April; at Avakubi, Chapin collected an adult male with somewhat enlarged testes on April 17; at Ibembo, Brother Joseph Hutsebaut collected a female with somewhat enlarged ovary on August 21. The period of nonbreeding activity in the northern part of the Congo forest is probably between November and early March; in the southern part it may be expected to be from June to September. Theoretically, there would be an equatorial band, in between, where the breeding and nonbreeding "seasons" would be difficult to distinguish. The presumed fosterers, the species of *Gymnobucco*, breed throughout a large part of the year, according to Chapin (1939, p. 512).

Breeding Habits

As to the breeding habits of the lyre-tailed honey-guide our ignorance is almost complete. At Medje, in the Belgian Congo, Christy collected a young *Melichneutes* scarcely ready to leave the nest, possibly taken from a nest of a brown barbet, *Gymnobucco*, but which was presumably brought to him by a native who did not relate where he found it. The inference that it came from a barbet's nest is pure guess, but seems very probable. Strictly speaking, however, we cannot say that *Melichneutes* is known to be parasitic like its relatives, but it would be surprising if it were otherwise. The brown barbet is very common at Medje.

Songs and Calls

Chapin (1939) noted that *Melichneutes* sometimes emits a hoarse chattering vocal note when sitting high up in a tree—a note apparently comparable to the chattering, guiding note of *Indicator indicator*, but slower. Chapin further informs me (in litt.) that a missionary in the Ituri district gave him to understand that the natives there claim that the lyre-tail comes around and makes a lot of noise when they are opening a bee-tree.

The most remarkable feature of the known part of the life history of this bird is the complicated aerial evolution it displays, which is accompanied by mechanical noises (nonvocal sounds) wholly comparable to the "bleating" of some snipe and other shore birds. The production of the sounds is apparently due to the peculiar form of the tail feathers. The two median pairs of rectrices are terminally curved laterally, the three outermost ones are very narrow and short, not unlike those of some species of snipe. In the Ituri forest, Belgian Congo, Chapin heard, throughout most of the year, "a reiterated note of tin-horn quality, the double syllables rising slowly in pitch, then dropping off, and repeated from twelve to thirty times. It may be heard afar, possibly at a quarter of a mile, and seems to come from above the forest canopy . . . From 1910 to 1914 I wondered what the bird could be; and then, on the occasion when I secured my only specimen of *Melichneutes*, I heard the strange noise given after a second bird of the species had flown off from the same high tree in the forest. It is almost certain that the nyêté is none other than our lyre-tailed honey-guide. The 'bleating' of certain species of snipe, it has been shown, is produced by their narrowed outer tail feathers during flight, by vibration of the webs as the air passes between them. Is it not likely too, that the nasal, tooting call of *Melichneutes* is made by the air rushing past the edges of the same feathers?"

Since Chapin's one view of the bird at Avakubi, Rougeot has made important additional observations at Oyem, in the Gaboon. He did see and hear the aerial evolutions on a number of occasions, but otherwise his experience was similar to Chapin's in that he more often heard but could not see the bird. Rougeot's latest observations (1951) are worth reporting in some detail. He found that the bird was to be heard on each of his excursions to a certain area in the forest. On one such trip, on April 2, he and a friend were in the forest along the road to N'Zorengone when they heard the lyre-tail noisily announcing his presence but did not see it. About noon they came out on the road to return home and noticed with surprise that the noise of the bird accompanied them for a distance of about two kilometers (they heard it nine times in all) up to the village of Keng-Akok, at the gates of Oyem. There the bird stopped and continued its sonorous evolutions, always remaining invisible.

On another occasion, in the same place, Rougeot heard it after 11 a. m., after the lifting of the mist that had covered the forest most of that morning. He noted that the first series of notes heard was incomplete and very feeble, audible at no more than 50 or 100 meters. The series was composed of three notes, *frrt . . . frrt . . . frrt*, and Rougeot concluded that this was but a grating of the feathers, lacking the sonorous quality they usually produce. He remarks that in February and March, when the sky is usually clearer than in the dry season, *Melichneutes* makes less noise than at other times of the year.

In his first paper Rougeot (1950, p. 63) writes that he never heard, or heard of, simultaneous calling from two lyre-tailed honey-guides, and hence was of the opinion that it was a bird of essentially solitary disposition. Yet Chapin's encounter with the bird involved two individuals together. In his second paper Rougeot mentions that on one occasion his native hunter told him that he had heard, at a nearby plantation, several of these birds calling ("talking indignantly") at the same time. Although he set out immediately for the spot, Rougeot failed to find or hear the species there.

The note which Chapin transcribes as *nyêté* Rougeot writes as *hein-hein*. He noted a maximum of 35 of these notes on one occasion, and writes that the sounds of increasing intensity are always more numerous than those of decreasing strength; on an average he counted five to nine of the former as against two to five of the latter per second. Each series was terminated by some powerful sonorous sounds characterized by an accelerated rhythm. The "calling" is usually most frequent from 8 a. m. until noon. Frequently, if not usually, the first syllable of the *nyêté* sound is more prolonged and lower in tone than the second, and at times may be entirely eliminated. There are usually 10 to 15 of these *nyêté* notes in a series.

Once Rougeot noted a lyre-tail flying like a woodpecker, opening its white-bordered tail both in soaring and in diving flight. Then it rested like a woodpecker on a branch, leaning on its tail which appeared somewhat forked, and then took off and disappeared.

To translate further from Rougeot's notes: On July 9, toward 10:45 a. m., a bird was seen flying slowly with a noticeable undulation at a low altitude; little by little it rose in the sky and made large spirals, and then larger and larger ones (the distances involved estimated by comparison with the largest trees nearby). At one moment it was seen flying with rapid wing beats, when suddenly it ended its ascent and hovered for an instant like a hawk about to swoop down on its prey, and then began to descend rapidly in a series of dives, like a series of large stairs. Then he heard, but far from the bird, under the same forested hills from which it reverberated, the extraordinary sound of the lyre-tail. This last—for such it was—went a little higher and the intensity of the vibrations diminished, and then it slid with increasing speed toward the forest where it disappeared and the amplified noise ended with the finish of the bird's descent. Then, by chance, another *Melichneutes* was seen, just an instant before it began its noisy fall; it dived, ascended again after a short horizontal flight, and again shot down toward the forest canopy with increasing speed, landed (apparently) and was lost to sight and sound.

A fortnight later, at the same place, Rougeot heard the bird swooping above the forest several times and finally saw it in the very gray sky at 9:30 a. m. It mounted in large, irregular spirals, beating its wings rapidly and descending with great speed after flying about horizontally for a time. However, there was a difference this time; the bird suddenly interrupted its noisy plunging, which was in loose, small spirals, to reascend silently and then to dive again farther away. Each time the *hein-hein* note was heard it corresponded well with the movement of the bird, but it was impossible at that distance to distinguish clearly what the bird was doing with its remiges and rectrices. A quarter of an hour later it rose a second time from the forest, and climbed very high, in spirals as usual, and then fell, noisily flapping its wings and spreading its tail. Six more performances were observed that morning. It was noted that the tail was opened widely during the noisy descents. The descent, usually preceded by a rather abruptly curtailed circling flight, was usually not quite straight, but also involved something of a spiral. The noise accompanying the descent is one that carries well beneath the forest canopy, above which the action is taking place.

The shortest duration of a complete soaring and diving performance varied from one to two minutes, the plunge itself not exceeding more than thirty seconds. The performance seems to take place chiefly on dark or overcast days; the bird mounts far into the air and then lets itself drop very swiftly, and as it descends it opens and closes its wings and tail rapidly, producing a sonorous vibration. While this noise is strong and carries well, it does not help one to find the position of its maker; it is very difficult to locate its author because its gliding is of dizzying speed. The accompanying diagrams of the paths of two such flight performances (fig. 6) are taken from Rougeot's paper.

The role of this performance is as yet uncertain. In other birds with comparable aerial evolutions, such as some snipe, larks, and others, there is often a connotation of courtship display involved. Thus, Armstrong (1942, pp. 255–256) mentions several different kinds of sounds produced mechanically by wing or tail feathers during such flights, and points out that while "the noisy flapping of agitated lapwings often appears to have an intimidatory rather than a courtship function . . . Other performances are more definitely in the nature of advertisement; the airy drumming of the snipe and the black-throated honey-guide . . . the humming glide of the southern dunlin, the roaring descent of the black-tailed godwit, and the boom of the American nighthawk . . . Often, but not always, there is a close correlation between display-flight and territory. The lark has the spacious and illimitable skies at his disposal and yet he is tethered by an invisible bond to a patch of ground."

The fact that Rougeot found the lyre-tail regularly in the same area makes one wonder if there may not be some suggestion of site tenacity or territoriality, even in a very loose sense, present here. Armstrong observes that high-flying vocal or mechanical displays are most characteristic of birds of the open types of country—tundra, prairies, etc. In this respect the lyre-tail is an exception.

As may be seen in our accounts of those species, two other honey-guides (*Indicator indicator* and *I. minor*) indulge in rustling flights, the precise meaning of which is not yet clear but which seem to be given by the males at or near the stud posts or song posts. In the lyre-tail, both sexes have the peculiar, specialized rectrices for such sound production, and both probably do go through the noisy aerial evolutions. As a matter of record it may be pointed out that in the case of Chapin's observation the male he shot did not go through any such aerial evolution and the bird that was with it and flew off (and which may have been a female) was heard to make the characteristic noise. It is therefore yet to be demonstrated that the male lyre-tail does actually produce the sound and go through the performance, but there can be little doubt that it does so.

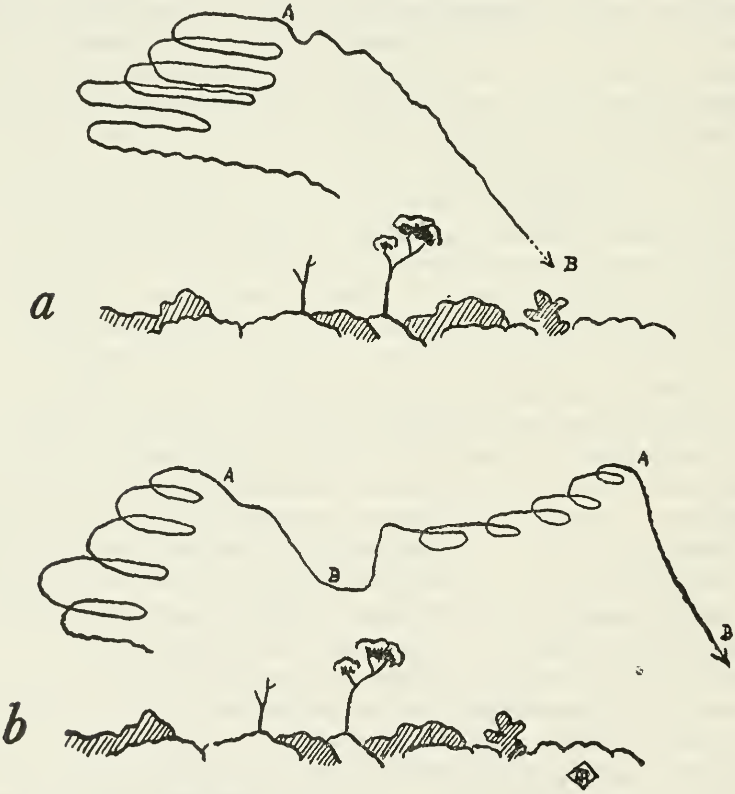

Figure 6.—Route of aerial evolutions of lyre-tailed honey-guide (after Rougeot): *a*, observation of July 9, 1950; *b*, observation of July 23, 1950. In each observation the part A–B is the diving part of the flight and is accompanied by the production of noise.

Rougeot (1950, pp. 62–63) suggests that the lyre-tail may live for part of the year in pairs, but this appears to be an assumption based on the thought that the two sexes may be able to communicate their whereabouts to each other by means of their noise-making proclivities. This cannot be accepted as factual.

Nestling Stage

As stated above we have no real evidence other than from analogy that the lyre-tail is parasitic, but, as Chapin and Rougeot state, there is little doubt that it lays its eggs in the nest holes of brown barbets of the genus *Gymnobucco.* However, all that is known is that at Medje, Ituri district, Belgian Congo, in April, a native hunter brought to Dr. Christy a nestling *Melichneutes,* with no evidence of what nest it came from. Chapin (1939, pp. 553–556) has examined this specimen and reports that it has a small white egg-tooth at the tip of the maxilla but shows no sign of there having been a hook on it and, similarly, no sign of any mandibular egg-tooth; the heel pad is well developed with pointed conical scales, as in young barbets and young indicators. The growing inner primaries show no sign of the reduction so frequent in young woodpeckers. The plumage stage of this bird would make it likely that it was too old to have retained the bill hooks even if it had had any originally.

Food and Feeding Habits

The adult male collected by Chapin had its gizzard filled with beeswax and small bits of insects, indicating a diet similar to that of the species of the genus *Indicator.* Bates found flakes of wax in the stomach of his specimen. Rougeot reports the stomach contents of his first specimen to consist of small granules of white, very hard wax together with unidentifiable remains of insects and fragments of the shell of an egg, the presence of which leads to the question as to whether the lyre-tail may supplement its diet by robbing the nests of small birds. In this connection it may be recalled that Skead (1951, p. 61), in the Cape Province, found *Indicator indicator* to do this on at least one occasion. A female from Ibembo, Belgian Congo, the body of which was kindly sent me for study by Dr. Schouteden, contained two species of ants, one spider, and some beeswax in its gizzard.

Description

This bird, sole member of the genus, resembles *Indicator* in its bill, which is slightly stouter in *Melichneutes,* and in its general form except for the tail, as mentioned in the description of the genus (p. 236).

Adult male (ex Chapin, 1915, pp. 512–513): Feathers of forehead, crown, back, and rump blackish brown, bordered or washed with yellowish citrine, those of nape and upper back whitish at the base. Sides of head lighter, shading gradually to olive-buff on throat, breast, and sides; middle of abdomen still lighter, ivory-yellow. Upper wing-coverts and secondaries fuscous-black (freshly molded feathers blacker) narrowly edged with olive-ocher. Primaries similar, but yellowish border almost entirely lacking; both primaries and secondaries fading to pale olive-buff on their inner edges. Under wing-coverts colored like the breast, but with faint dusky shaft-streaks. Feathering of flanks ivory-yellow, those of the tibiae with strong blackish median lines. Two middle pairs of rectrices dull blackish; third pair whitish, with a small blackish spot on the outer edge close to the tip, and a larger concealed black spot on the inner web towards the base; the three remaining pairs of rectrices white. The long median pair of under tail-coverts blackish, the next pair similar, but margined with whitish, the remainder ivory-yellow with faint shaft-streaks of dark brown. Upper tail-coverts fuscous-black, bordered with amber-yellow.

The bill, nostril, and feet resemble those of *Indicator indicator*, but the bill is somewhat stouter, while the wings and tail are shorter. The ninth (outer) primary is intermediate in length between the sixth and fifth, and the seventh and eighth are longest.

Iris bright brown, naked edges of eyelids grayish brown; bill dusky brown; feet dull grayish green.

Measurements in millimeters: wing 93.5, tail 56, culmen from base 13.5; tarsus 14.

Adult female: Similar to the adult male but with the longest under tail-coverts shorter, not extending beyond the angle of the fork made by the laterally curved median rectrices. Measurements in millimeters: wing 96, 94, tail 51, 53, culmen 12.5.

Juvenal (ex Reichenow, 1910, p. 160; description of "*M. sommerfeldi*" (= young *robustus*)): Top of head black, the individual feathers brownish black with dark black edges; the sides of the head deep black; the underparts of the body from the throat to the abdomen dark olive brown, darker anteriorly, the throat almost black; lower abdomen and under tail-coverts cream colored with dark brown tips, the longest under tail-coverts dark brown with cream colored edges; upperparts of body and upper wing-coverts dark brown washed with olive yellow, the individual feathers having dirty olive-yellow tips; remiges blackish brown, externally edged with olive yellow, internally with cream color; under wing-coverts cream color with dark brown terminal edges; the median tail feathers brownish black, the outermost yellowish white; bill and feet blackish, the base of the bill pale.

A younger bird, supposedly taken from a nest, is described by Chapin (1939, pp. 553–556) as follows: Crown and cheeks sooty, wings dusky with olive-green edgings, back and rump more greenish than crown; underparts dark grayish olive, washed with blackish; abdomen and under tail-coverts (except the longest ones) lighter and greener; rectrices, though only half grown, are colored much as in the adult, and the middle ones curve outward slightly; bill largely black.

Nothing has been written on the molts of this bird. Bates's type, an adult female, still has a few scattered blackish feathers from the juvenal plumage on the breast, suggesting that this area is the last to molt.

Native Names

Following is a list of names by which this species is known to the natives.

Name	*Tribe*	*Locality*
Amazeke	Mambuti	Belgian Congo (Ituri)
Kumu-kumu	Babali	Belgian Congo (Ituri)
Mobum	Fang-ntumu	Spanish Guinea
Ngebu-ngebu	Bandaka	Belgian Congo (Ituri)
Nvebe	Fang-ntumu	Spanish Guinea
Nyeté	Azande	Belgian Congo (Nepoko area)
Pemé-pemé	Mabudu	Belgian Congo (Ituri)
Pemu-pemu	Bandaka	Belgian Congo (Ituri)
Pupu-puru	Babali	Belgian Congo (Ituri)
Selem n'gomo	—	Gaboon
Vébek	Bulu	Cameroon
Vébeu	—	Gaboon

Genus *Melignomon* Reichenow

Melignomon Reichenow, Ornith. Monatsb., vol. 6, p. 22, 1898. (Type, by original designation, *Melignomon zenkeri* Reichenow.)

Similar to *Indicator* except in its bill, which is small and slender, approaching that of *Prodotiscus*, but with narrow, slitlike nostrils (not open and rounded as in *Prodotiscus*); differs from *Prodotiscus* in having 12 tail feathers, the outermost pair of which is conspicuously shorter than the others (which are fairly equal). Possibly not more than a subgenus of *Indicator*.

Monotypic; forest of the Lower Guinean region, Cameroons to Belgian Congo.

Zenker's Honey-Guide

Melignomon zenkeri Reichenow [67]

FIGURE 1; PLATE 21

The least known of all the African honey-guides, this species occurs in the dense evergreen forest from Yaunde in eastern Cameroons and Ebebiyin, N'kumadjap, in Spanish Guinea eastward across the Congo forest to the Semliki Valley. Peters (1948, p. 65) states that it may possibly range south to northwestern Angola, but I know of no evidence of its presence there.[68] As far as I know, no European has ever seen this species in life, all the known examples having been collected by native assistants. The localities from which the species has been recorded are few in number: CAMEROONS: Bitye and Esamesa on the River Ja, Yaunde; BELGIAN CONGO: Kotili on the Itimbiri River, Ibembo, and Beni, on the western edge of the Semliki Valley; SPANISH GUINEA: Ebebiyin, N'kumadjap forest, very close to the Cameroons frontier.[69]

A female shot at Esamesa, Cameroons, in January was in breeding condition; another collected nearby at Bitye, April 17, was in fairly fresh plumage, probably a postbreeding bird.

In the gizzard of the first specimen procured by Bates's helpers were particles or fine flakes of beeswax mixed with some tiny black particles, probably bits of insects. Bannerman (1933, p. 418) mentions these black particles as "small black insects like ants and winged termites" but this seems to be only a needless guess.

The natives in Spanish Guinea know very little of the various honey-guides, and even less of this one. When questioned by Sabater, they called it "mé," a name used for all the honey-guides except the lyre-tailed one. The natives belonged to the Fang-ntumu tribe.

DESCRIPTION

ADULT (sexes alike): Entire upperparts olive-brown, the crown faintly tinged with olive, the feathers of the back and wing-coverts as well as the secondaries and most of the primaries narrowly edged with olive-yellow; middle pair of rectrices dark brown with faint olive-yellow margins, remaining rectrices white tipped with light brown, which color extends all the way along the margin of the outer webs; entire underparts pale grayish brown strongly washed with yellow; under wing-coverts pale brownish; iris brown, bill blackish,[70] feet dull greenish yellow. Measurements in millimeters: male: wing 79–83, tail 48–52, culmen 9–10, tarsus 16; female: wing 73–76, tail 46–49, culmen 9, tarsus 10–13. Two males and three females were measured. (Bannerman, 1933, p. 418.)

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[67] *Melignomon zenkeri* Reichenow, Ornith. Monatsb., vol. 6, p. 22, 1898. (Jaunde, Cameroons.)

[68] The basis on which Peters included northwestern Angola in the range appears to be a specimen collected by Braun. However, the specimen, now in the British Museum, was wrongly identified and is really *Prodotiscus insignis*.

[69] One specimen, collected in January 1953 by G. Sabater's native assistants, unfortunately was destroyed by insects after it was put away for shipment to the United States. In view of the mistaken identification of Braun's Angola bird, it is possible that this record also may be looked upon as uncertain since the bird was not examined by an expert ornithologist.

Other plumages are unknown.

Genus *Prodotiscus* Sundevall

Prodotiscus Sundevall, Öfv. Vet. Svenska-Akad. Forh., vol. 7, p. 109, 1850. (Type, by monotypy, *Prodotiscus regulus* Sundevall.)

Hetaerodes Cassin, Proc. Acad. Nat. Sci. Philadelphia, vol. 8, p. 157, 1856. (Type, by monotypy, *Hetaerodes insignis* Cassin.)

The most divergent of all the honey-guides; small in size, with only 10 tail feathers, the outermost pair somewhat shorter than the others, the plumage generally looser and fluffier than in *Indicator*, and the bill small and slender, the skin thinner (not noticeably thick as in the genus *Indicator*), the sternum with a much deeper keel than in any of the other genera (which are generally of a dorsoventrally depressed body form). The birds of this genus, unlike all their relatives, do not feed regularly on bee comb and its inclusions but are insect-catchers, feeding largely on scale insects. Furthermore, they differ markedly from the other honey-guides in that they often lay their eggs in the open, cuplike nests of such birds as warblers (*Apalis*), white-eyes (*Zosterops*), and flycatchers (*Platysteira*). These hosts are known as yet for only one species, *P. insignis;* the meager evidence for the other, *P. regulus*, suggests a hole-nesting host, *Petronia superciliaris*.

Two species; one (*insignis*) in the forests from Upper Guinea to southern Ethiopia, south to Southern Rhodesia; the other (*regulus*) in the dense bushveld from Cameroons to Ethiopia, south to Natal and the eastern Cape Province. The forest species (*insignis*) is olive green in color, the bird of the more open country (*regulus*) is dull brown. According to Benson (1953, p. 45), in Nyasaland the two species overlap ecologically, both being found in *Brachystegia* woodlands.

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[70] Bates (1911, p. 504) writes that two birds from the Cameroons had the bill dark horny, yellowish at the base of the mandible and at the gape; the nostrils with a long, elliptical raised rim.

Slender-Billed Honey-Guide

Prodotiscus insignis (Cassin)[71]

Figure 1; Plate 21

Distribution

The slender-billed honey-guide occurs in primeval and also in secondary forests and in gallery forests from Sierra Leone, Liberia, Ivory Coast, Gold Coast, Togoland, Nigeria (once found in open tree savannas), the Belgian Congo, Uganda, and Angola, eastwards to Kenya Colony, southern Ethiopia, Tanganyika Territory, Nyasaland, Northern and Southern Rhodesia. Its altitudinal range is from close to sea level up to as high as 7,000 feet (Limuru, Kenya Colony). In the vast region it occupies it has become differentiated into four currently recognized races, as follows.

Prodotiscus insignis flavordorsalis Bannerman:[72] Sierra Leone (Kwendu), Liberia (Ganta), Ivory Coast (Beoumi), Gold Coast (Ejura and Goaso, Ashanti), Togoland, and southwestern Nigeria (Abeokuta).

Prodotiscus insignis insignis (Cassin): South-central Nigeria (Benin (identification to subspecies based on a drawing and measurements, the specimen having been destroyed by a dog), Alayi, Owerri), Cameroons (Efulen, Okoa, Kumba, Esamesa, Nko'olong, River Ja, Bitye), Gaboon (Camma, Moonda River), across the Belgian Congo, from the lower Congo eastward to the Uelle, Ituri, and Semliki Valleys, and west of northern Lake Tanganyika, to Uganda (Bwamba, Wadelai) and to western Kenya Colony (Kakamega, Yala River). Also, but subspecies uncertain, south in the Rift Valley to north-central Tanganyika Territory (Oldeani Bush). In the eastern part of its range this race seems to be limited on the east by the Rift Valley, east of which it is replaced by the next form. There is some question as to its western limits in Nigeria, as the subspecies *flavodorsalis* is recorded from Abeokuta and the nominate form from Benin and Owerri. Benin is only about 200 miles east of Abeokuta.

Prodotiscus insignis ellenbecki Erlanger:[73] Southern Ethiopia (Daroli, Arussi-Gallaland, and Uanda, south of Addis Abeba), Kenya Colony east of the Rift Valley (Karura, Langata, and Ngong forests in the Nairobi area, Limuru, Thika, Kibwezi, Kyambu, Nyeri, western slopes of Mount Kenya), and northeastern Tanganyika Territory (the Kilimanjaro region (Moshi) and the Usambara Mountains).

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[71] *Hetaerodes insignis* Cassin, Proc. Acad. Nat. Sci. Philadelphia, vol. 8, p. 157, 1856. (Moonda River, Gaboon.)

[72] *Prodotiscus insignis flavordorsalis* Bannerman, Bull. Brit. Ornith. Club, vol. 43, p. 161, 1923. (Béoumi, 650 feet, Ivory Coast.)

[73] *Prodotiscus ellenbecki* Erlanger; Ornith. Monatsb., vol. 9, p. 182, 1901. (Daroli, Arussi Country.)

Prodotiscus insignis zambesiae Shelley: [74] Central southern Belgian Congo, from Tembwe on Lake Tanganyika and the Upper Katanga (Elisabethville, and Kasaji on the Lualaba) south to southern Angola (Quipungo, Quicolungo,[75] Cabeça de Ladrões), across Northern Rhodesia (Lunge, near Kasempa, Luanshya, Kabompe, Mwinilunga, Balovale) to Nyasaland (Nehisi Mountain, Kota-kota District, Mlanji, Karonga District, Mombera District, Chinteche—1,700–5,000 feet), Mozambique (Chole and Masuku Mountains, Mzimba, Unangu) and Southern Rhodesia (Gatooma, Bindura District, Makwiro, and near Salisbury).

These races differ from each other in the following particulars. The entire upperparts are strongly washed with golden, brightest on the rump, and the underparts are lighter brown, faintly tinged with olive in *flavodorsalis;* the nominate race has the crown dusky brown tinged with olive, the rest of the upperparts olive brown, and the entire underparts ashy brown with an olive tinge on the breast and sides; the subspecies *ellenbecki* resembles *insignis* but has the back and the upper wing-coverts olive gray, the forehead, neck, and breast brownish gray, the under tail-coverts white, while the southern race *zambesiae* differs from *insignis* in having the sides of the face and throat pale gray, and the whole of the abdomen and under tail-coverts white instead of dingy olive brown.

Breeding Range and Season

The data indicative of breeding dates and localities known to me are as follows:

Gold Coast: Goaso, Ashanti, December 28, female with a soft shelled egg in oviduct, "just starting to breed"; January 1, a male taken, showed testes beginning to enlarge. (Subspecies *flavodorsalis.*)

Cameroons: Esamesa, River Ja, January 29, juvenal female, probably still attended by its foster parents; Kumba, November 7, adult female with two large yolking ovarian eggs. (Subspecies *insignis.*)

Ethiopia: Daroli, near Ginir, Arussi-Gallaland, February 17, female in breeding condition. (Subspecies *ellenbecki.*)

Kenya Colony: Nyeri, May 2, female with well developed ova; Limuru, December 31, young fledgling fed by *Zosterops* sp., Ngong, June and July, nestlings in nests of *Zosterops* and *Platysteira*; Mau,

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[74] *Prodotiscus zambesiae* Shelly, Ibis, ser. 6, vol. 6, p. 8, 1894. (Zomba, Nyasaland.)

[75] Subspecies uncertain; only specimen from northern Angola is immature.

May, nestling in nest of *Zosterops*. Also said to breed in August (Mackworth-Praed and Grant, 1952, p. 748). (Subspecies *ellenbecki*.)

Nyasaland: Chole Mountain, September 2, female, whose ovary indicated it was "coming up fast to breed"; Mzimba, June 12–30, five males and one female, all with gonads somewhat enlarged; Maruku Mountain, August 14, female with somewhat enlarged ovary. (Subspecies *zambesiae*.)

Mozambique: Namuli Mountain, August 6, female "just starting to breed"; male taken August 2 showed testes starting to swell. (Subspecies *zambesiae*.)

Southern Rhodesia: Gatooma, December 21, female with well developed egg in oviduct. (Subspecies *zambesiae*.)

Angola: Northern part, no date, parasitizes *Apalis rufogularis*.

Courtship and Mating

The Bensons (1948, p. 392), at Blantyre, Nyasaland, in September, observed one of these birds flying about the tree tops "uttering a very harsh *skeee-aaa* (*e* as in 'seen', *a* as in 'bad'), repeated several times at intervals of about one second. Probably a breeding display. Normally quite silent and flight unspectacular." A similar observation was made by Benson (1952b, p. 151) in the Dzalanyama Mountains, Nyasaland, late in May. Mr. J. G. Williams, Nairobi, sends me a note on what may have been a display by this bird in the Karura forest, near Nairobi. On this occasion one bird (presumably the male?) approached a second one (female?) to within two feet, and then commenced to nod its head up and down, at the same time puffing out the feathers of its rump and back, so that the two patches of white feathers which lie along each side of the lower back, and which are usually hidden, became very conspicuous. Both birds flew away right after this and were not seen again. In neither case were the birds collected to ascertain their sex.

These two observations constitute the whole of our present information; the latter of the two (by Williams) seems definitely a courtship performance, the former is less certain in its implications, especially as no second bird was seen to be present. I have never met with this species in the field, but in the related *Prodotiscus regulus* I have never seen any similar behavior. In the genus *Indicator* (*I. indicator* and *I. minor*, at least) the males do have a circular rustling flight, but the sound is mechanical and not vocal.

Williams writes me that he has never seen any evidence pro or con bearing on any territorialism in this species.

Songs and Calls

Like most other portions of the life history of this bird, its vocalisms are imperfectly known. No one has yet studied the species sufficiently to be able to say which sounds are produced only by males or only by females or what their various functions may be. For the present all that can be done is to assemble the few available data.

In Kenya Colony, Williams writes me that he has usually found this bird to be a silent creature, but occasionally had heard it give a short, low chattering note. Vincent records a subdued squeaky chatter from this bird in Mozambique; Marchant once heard a weak *whi-hihi* from one in Nigeria.

As mentioned in the discussion of courtship behavior, the Bensons heard a bird in flight give a very harsh two-syllabled call *skeee-aaa* repeated a number of times at short intervals as it flew.

Eggs and Egg Laying

Mackworth-Praed and Grant (1952, p. 748) describe an oviduct egg of the southern race *Prodotiscus insignis zambesiae* as white and about 15 by 12 mm. The circumstances attending this observation appear to be unpublished and are unknown to me.

Hosts or Victims

This little honey-guide is very different from the species of the genus *Indicator* in its known selection of foster parents for its offspring. Whereas all of the latter parasitize hole-nesting birds almost exclusively, the present one deposits its eggs in the small, open, cuplike nests of white-eyes, flycatchers, and warblers. There are no published data on the victims of *Prodotiscus insignis* other than an unsupported statement by Roberts (1940, p. 182) to the effect that the southern race *zambesiae* is "presumed to be parasitic" on *Petronia superciliaris* and one by Mackworth-Praed and Grant (1952, p. 748) that the same race is parasitic on white-eyes, rock sparrows, and tinkerbirds. I do not know of the evidence behind the parts of these statements having to do with rock sparrows and tinkerbirds. The few observations given below are, obviously, only a beginning of what is still to be discovered about the hosts of this bird.

Platysteira peltata peltata Sundevall. Black-throated wattle-eye.

Platysteira peltata Sundevall, Öf. Svenska Vet.-Akad. Förh. Stockholm, vol. 7, p. 105, 1850. ("Caffraria inferiore"; type from Umlalaas [i. e., Umlezi] River, near Durban.)

One record kindly sent me by Dr. van Someren, who found a nest of this flycatcher at Ngong, Kenya Colony, in July, containing a young *Prodotiscus insignis ellenbecki* as its sole occupant.

Apalis rufogularis angolensis (Bannerman). Angola red-throated forest-warbler.

Euprinoides rufigularis angolensis Bannerman, Bull. Brit. Ornith. Club, vol. 43, p. 30, 1922. (N'dalla Tando.)

One record, unfortunately merely a bare statement without further details.

Rudolf Braun (in litt. to J. P. Chapin) reports that this warbler is a host of *Prodotiscus insignis* in northwestern Angola.

Zosterops virens kikuyuensis **Sharpe.** Kikuyu green white-eye.

Zosterops kikuyuensis SHARPE, Ibis, ser. 6, vol. 3, p. 444, 1891. (Kikuyu, Kenya Colony.)

Van Someren informs me that at Ngong, Kenya Colony, in June (1949?) he found a nest of this race of the green white-eye containing two young *Prodotiscus insignis ellenbecki.* In May 1953, in the same place, he found another nest containing one young slender-billed honey-guide.

Zosterops virens jacksoni **Neumann.** Mau green white-eye.

Zosterops jacksoni NEUMANN, Ornith. Monatsb., vol. 7, p. 23, 1899. (Mau.)

A nest at Mau, western Kenya Colony, containing a young Ellenbeck's slender-billed honey-guide was found in May by van Someren, to whom I am indebted for this information.

One other record, unfortunately not identified to host except that it was a form of *Zosterops,* reported to me by J. G. Williams is as follows: A young fledgling Ellenbeck's slender-billed honey-guide, collected by a school boy at Limuru, Kenya Colony, December 31, was being fed by a pair of unidentified white-eyes, according to the collector.

Questionable Host Records

In addition to these few records it may be noted that Benson (1951, p. 91) found a nest of *Campethera bennettii bennettii* (Smith) at Mzimba, Nyasaland, containing one very small white egg measuring 18.4 by 15.3 mm. (considerably smaller than an unquestionable, oviduct egg of the woodpecker). Benson suggests it may be a honey-guide's egg, and that of all the possible species, *Prodotiscus insignis* is the most likely and is one that was actually seen in that locality. Such an indefinite observation hardly merits further discussion. More recently Benson (1952b, p. 151) has withdrawn his earlier suggestion and assumes that either *Indicator minor* or *I. exilis meliphilus* may have been involved!

Still more recently Benson (1953, p. 45) lists the southern double-collared sunbird, *Cinnyris chalybeus,* as a possible host in Nyasaland. However, this is based solely on the fact that he saw a sharp-billed honey-guide chased twice by a male sunbird near a nest of the latter.

Food and Feeding Habits

The two species of *Prodotiscus* not only do not guide to bees' nests, but, unlike the species of *Indicator,* do not eat beeswax regularly or even get other food from bees' nests. The following data, culled from the published observations and from the information kindly supplied by correspondents show that this species feeds largely on scale insects, but also on other forms of insects and fruit.

Moreau (in Sclater and Moreau, 1932, p. 666) obtained four specimens at Amani, Tanganyika Territory, and found in their gizzards quantities of scale insects and their waxy exudation. In a single case of the four there were predatory beetle larvae. Moreau comments on the fact that it is quite extraordinary for an insectivorous bird to be so specific in its diet. In Kenya Colony, Williams (in litt.) informs me that in a number of individuals collected he found remains of scale insects, lepidopterous larvae, and unidentified insects or spiders, and an unidentifiable orange waxy substance. The van Somerens (1949, p. 43) found this honey-guide at Bundibugyo, Bwamba forest, western Uganda, flitting around an *Erythrina* tree where it appeared to be disturbing insects among the foliage and flowers and then catching them in flight. They "were interested in this behavior for it contrasted very much with the feeding habits . . . in the Nairobi-Ngong district of Kenya, where the principal food is scale insects and mealy bugs." They also noted the species twice in low *Gymnosporia* trees in full bloom, "to which myriads of small hymenopterous insects and Diptera were attracted." Also in the Bwamba forest, Williams saw the species singly or in twos, especially with the sunbird *Anthreptes fraseri axillaris* (Reichenow). Its appearance was rather like a tit, and it would sometimes hang upside down while feeding.

Williams writes me that in the dry Kenya highland forests he has watched this species exploring lichen-covered branches, bunches of *Loranthus*, and similar objects, apparently seeking small insects and spiders. He has "watched the birds feeding on something they got off lichened branches, perhaps scale insects (?), and once . . . saw one eating ripe berries of *Loranthus* sp., together with *Zosterops*."

In the Belgian Congo, Chapin (1939, pp. 535–536) found some soft material that may have been caterpillar remains in the gizzard of a specimen, and Marchant (1951, p. 74), in Nigeria, found green limpet-shaped objects which might have been "shield bugs" in his example. In the Mwinilunga district, Northern Rhodesia, White (1946, p. 73) recorded unidentified insect remains in the gizzard of a bird he collected. In Southern Rhodesia, Edwards (in litt.) saw one at Gatooma, acting much like a bush warbler (*Eremomela scotops*), creeping about the higher branches of the trees in search of insects and occasionally flying out and catching insects on the wing like a flycatcher. Townley also noted the species hawking about after insects like a typical flycatcher, and found remains of small beetles and other insects, but no trace of wax or bees, in their gizzards. In Nigeria, Marchant (1953, p. 51) found insects (other than hymenoptera) and unidentified limpetlike objects in a gizzard of one of these honey-guides. In Nyasaland, Loveridge (in Peters and Loveridge, 1953, p. 108) saw one feeding on termites flying about after a prolonged rain. Serle (1954, p. 60) watched one hunting silently for insects among the leaves and twigs of an albizzia tree in the Cameroons. He reports that the species eats fruit as well.

Some observers—J. Vincent (1935, pp. 14–15), Winterbottom (1942, p. 361), and Williams (in litt.)—have found this honey-guide to be a member of occasional mixed bird parties where food was available in reasonable quantities.

It might be mentioned, for greater accuracy, that the observations from Kenya Colony and Tanganyika Territory refer to the subspecies *ellenbecki* (including *reichenowi*), those from Nigeria, the Belgian Congo, and the Bwamba forest (extreme western Uganda) pertain to the nominate race, while the data from Mozambique, Southern Rhodesia, and Northern Rhodesia have to do with the form *P. i. zambesiae.*

All that is known of the food of the young is that the fledgling collected December 31 at Limuru, Kenya Colony, said to have been still attended by a pair of *Zosterops* sp., had a mass of small oval seeds with orange pulp and a few small lepidopterous larvae in its gizzard.

As in the case of other parasitic birds, there is no reason to suppose that the nestlings receive any food except that normally given to their own young by the species of birds victimized.

Miscellaneous Behavior

The flight of this species is undulating, and the dips in the flight are often accompanied by flashing of the tail, i. e., momentary spreading of the rectrices, which renders the white outer feathers very conspicuous.

When perched on a twig the bird looks much like a small flycatcher. In Nigeria, Marchant (1951, p. 74) saw one in a tall bush, flitting quickly from twig to twig and, when perched, flicking its tail from side to side like a flycatcher. Another individual quietly foraged about in the leaves like a titmouse.

It has been found, in mixed bird parties in the trees, with species of *Zosterops*, *Apalis*, and *Campephaga*. While as many as three individuals have been seen together (once, by Williams), generally, "a pair may be seen in these bird parties" (Williams).

In Nyasaland, Benson once saw one of these honey-guides being chased about several times by a male sunbird, *Cinnyris chalybeus*, a species that was nesting locally at the time. Whether the *Prodotiscus* had ventured too near to a nest is, of course, not known.

DESCRIPTION

Prodotiscus insignis insignis

ADULT (sexes alike in coloration): Forehead, lores, crown, and occiput olive brown, slightly tinged with olive; upperparts of body and wings similar but more intensely tinged with yellowish olive to ecru olive, this wash being brightest and most pronounced on the lower back and median part of the rump, the lateral parts of the rump and the flanks with longer, silky white feathers; upper wing-coverts and remiges olive brown edged with yellowish olive, the primaries more narrowly edged with olive externally than the secondaries, all the remiges internally incompletely edged with whitish; upper tail-coverts olive brown edged and washed with yellowish olive, the shortest ones tipped with olive ocher, the longest ones almost wholly olive brown; median two pairs of rectrices dark olive brown; lateral three pairs wholly white; chin and throat ashy pale buff, the breast and sides slightly darker—ashy pale light drab, abdomen becoming more ashy, less brownish, and becoming paler, more whitish posteriorly; under tail-coverts white with a very faint tinge of pale drab or pale buffy gray; under wing-coverts pale, whitish tinged with olive drab; iris dark brown; bill blackish with a little pale greenish yellow at the corners of the mouth; tarsi and toes dusky greenish slate to dark gray. Measurements in millimeters: males: wing 62–65, tail 40–44, culmen from base 8–9, tarsus 12; female: wing 61, tail 39–42, culmen from base 8, tarsus 11–12.

JUVENAL (sexes probably alike): Similar to the adult but generally duskier above, the greenish wash and margins of the feathers less pronounced.

NATAL DOWN: Not known, if any.

The plumage differs in the other subspecies as follows.

Prodotiscus insignis flavodorsalis: Brighter in color, the entire upper surface washed with golden, and the feathers of the rump with particularly bright yellow tips. Measurements in millimeters: male: wing 67, tail 42, culmen 8, tarsus 12.5; female: wing 64, tail 44, culmen 8, tarsus 12.5.

P. i. ellenbecki: Larger, and paler and grayer on the breast, with the under tail-coverts purer white. Measurements in millimeters: male: wing 69–73, tail 53, culmen 10, tarsus 11–12; female: wing 68, tail 47, culmen 9, tarsus 11. Weight: male 16.5 grams, female 12.1, 12.3 grams, *P. i. zambesiae:* Still longer winged, slightly lighter in color throughout than the nominate race, the crown gray with little or no greenish wash, the underparts slightly paler than in *P. i. ellenbecki.* Measurements in millimeters: male: wing 74, tail 48, culmen from base 8.2, tarsus 11; female: wing 73, tail 49, culmen from base 8.3, tarsus 11.

Sharp-Billed Honey-Guide

Prodotiscus regulus Sundevall [76]

Figures 1, 2,*h*, 3,*h;* Plates 20, 23

Distribution

The sharp-billed honey-guide is found in the fairly dense to fairly open bushveld and even in the semiarid areas, and, in South Africa, has adapted itself to the wattle plantations as well. It is chiefly a bird of the eastern parts of Africa from southern Ethiopia and Sennar south to the eastern Cape Province, but also occurs westward to Bosum (or Bozoum) in French Equatorial Africa, the Banso highlands of British Cameroons (only one record from the former area and but three from Cameroons), and in Angola. In the Anglo-Egyptian Sudan it appears to have been recorded only from the Blue Nile (Geraf, Famaka, and near Roseires, in Sennar); in Ethiopia it has been collected at Unji on Lake Zwai, on the Gato River near Gardulla, at Yavello, Harar, and Ghinir on the Daroli River. In Kenya Colony scattered locality records are more numerous—Campi-ya-bibi, Chyulu Hills, southern Guaso Nyiro, Nairobi, Thika, Mtito Andei, Samburu, Naivasha, the Bura Hills, Teita, and the Lorogi Plateau; while in Uganda it has been taken at Burumba in Ankole, but not elsewhere to my knowledge. Tanganyikan records are available from Kilimanjaro, Mount Meru, Sumbawanga, Morogoro, and Apis Rock, and south to Mbisi, near the southeastern part of Lake Tanganyika. In the Belgian Congo the species is known as yet only from Tembwe west of Lake Tanganyika, Boudewijnville, Kasaji, Dilolo, the Upemba Park, and from Kabalo on the Lualaba River. Data from Mozambique are almost nonexistent, although the bird must occur in many areas there; I know of one example taken at Lorenço Marques now in the museum in that city. More is known of its occurrence in Nyasaland whence there are definite records from Bua River in the Lilongwe District, Mpimbi, Dowa District, Mzimba highlands, near Fort Johnston, Zomba, and near Liwonde. In Angola specimens have been taken at Gambos and Caconda; and in Northern Rhodesia at Shiva Ngandu near Lake Young, Namusonde, Namwala, at Chilanga near Lusaka, at Lofu River, Chalimbana, at Tembwe, Lundazi, at Chiromwe, along the middle Zambezi, Danger Hill near Mpika, and the Pempele Pool on the Mwinilunga-Congo border. The bird undoubtedly occurs in many parts of Southern Rhodesia, but I know of only three actual specimen records from that country—from Glenara, 12 miles north of Salisbury; from the Lundi River, between Fort Victoria and Beit Bridge, where one was taken by Plowes; and another taken by Plowes in the Matopos Mountains (there are sight records from Gatooma and from Rumani Estate). From Bechuanaland Protectorate it is known from Tsotsoroga Pan. Farther south, in the Union of South Africa, there are many records from the Transvaal, Zululand, Natal, and the eastern Cape Province. I am aware of no authentic records of its occurrence in the western portions of the Cape Province, or in the South-West African Protectorate. A specimen in the Leiden Museum is labeled as from the latter country, but it is from Gambos (Kellen collection), which locality appears to be north of the Cunene River, and is therefore in southern Angola.

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[76] *Prodotiscus regulus* Sundevall, Öfv. Svenska Vet.-Akad. Förh., vol. 7, p. 109, 1850. ("Caffraria inferiori et superiori," type from Mohapoani, Witfontein Berge, western Transvaal.)

The altitudinal range of the sharp-billed honey-guide is from near sea level up to at least 6,600 feet at Ndu, British Cameroons, 6,000 feet at Lorogi Plateau, Kenya Colony, and 6,500 feet in the Drakensberg Mountains, Natal.

Throughout this extensive range the species has not become differentiated into any recognizable races. Two subspecies, *camerunensis* from the Cameroons and *peasei* from Ethiopia, have been named, but neither prove to be valid forms. The recently proposed *adustoides* from Natal requires confirmation before it can be accepted.

Seasonal Movements

As in the other honey-guides, the present species is not migratory in a geographical sense, but there may be some local movements. Thus, near Howick, central Natal, in October and early November 1924, I found the species much commoner than the literature or the experience of other observers had led me to expect. In the course of two weeks I collected five specimens and every one was found, on dissection, to be a male. It was not until some weeks later, after I had left that area, that my friend Rodin Symons obtained a female there. This experience suggested that there might have been a small-scale migration and that the males arrived before the females, but it is not to be looked upon as more than a suggestion. Some years later (Friedmann, 1930b, p. 100) in summarizing the then existing data, it was stated that "when a species known to be rare throughout its range suddenly appears in fair numbers in the spring that fact may be looked upon as suggestive of a migratory movement. When, on top of this, it is found that all the individuals are of one sex—males, and that not until some time later do the females appear, the migration hypothesis seems the only one able to account for all the facts involved.'' However, in 1950 I went back to the same area, but earlier in the season, and found *Prodotiscus regulus* still there while it was still winter (end of August). In addition, the first sharp-billed honey-guide that I collected proved to be a female. The bird cannot therefore be said to be migratory in any regular sense, but it still seems not improbable that the 1924 experience did reflect some local influx of males.

Recently some additional evidence of this sort has come to me from W. L. Chiazzari, who writes me that in the Richmond District, Natal, "there did appear to be some fluctuation in the numbers which assumed a seasonal character, but at no time, winter months included, was it entirely absent." On the other hand, at King William's Town, Skead has observed it in every month of the year.

Breeding Range and Season

In view of the fact that no one has yet found an egg or a nestling of this species, the data relevant to breeding are very scanty and are all from the southern part of its range, as follows:

Belgian Congo: Upemba Park, October 28, male with enlarged testes collected.

Northern Rhodesia: Shiwa Nganda near Lake Young, October 11, male collected, gonads becoming enlarged, "soon to breed."

Southern Rhodesia: Rumani Estate, January 10, honey-guide reported seen leaving nest of *Petronia superciliaris*, one small white egg (*Prodotiscus*?) in nest. (Townley; in catalog of C. D. Priest egg collection in Victoria Memorial Museum, Salisbury; specimen not to be found in 1951.)

South Africa: Mooi River, central Natal, March 11, a fledgling seen for two days attended by a pair of *Petronia superciliaris;* Richmond, Natal, February 5, adult *Prodotiscus* seen leaving a nest of *Apus caffer* (in an old nest of *Hirundo cucullata*), but which did not contain an egg attributable to *Prodotiscus.*

Courtship and Mating

In central Natal, Vincent (in Roberts, 1930) noted that in spring and summer "both birds of a pair will fly forth and flit erratically round at a very considerable height, one chasing the other and uttering the while a loud and rasping *zeet, zeet,* finally to settle on the topmost branches of a high tree."

Near Kei Road, eastern Cape Province, on November 9, I saw two sharp-billed honey-guides in an acacia tree. One, apparently the male, was displaying to the other, presumably a female. The first bird was perched about 10 inches from the second one; it fluffed out its body feathers, especially the white flank patches, which became quite conspicuous as it drooped its wings in a half-open position, the white flank patches extending above the lowered level of the wings; its tail was spread showing the white on the outer rectrices very plainly. It bent its head downward, and gave a sibilant *zzzz.* The other bird (female?) took no apparent notice, but as I moved to get a different view she (?) gave a sharp *zeeep* note and flew off in an undulating flight, followed by the male (?). A strong wind came up, making it difficult to keep track of the birds, and I did not find them again.

Eggs

One egg, "possibly" of this species, measuring 18 by 15 mm. in a nest of *Lybius torquatus* reported by A. Roberts (1939, p. 105) is too uncertain to be accepted. One "small white" egg, supposedly of this species, in a nest of *Petronia superciliaris* is reported by Townley from Rumani Estate, Southern Rhodesia.

Hosts or Victims

The only definite knowledge we have so far as to the victims or hosts of the sharp-billed honey-guide is the following note published by J. Vincent (1935, p. 16).

> On 11 March, 1930 . . . on my farm [near Mooi River] in Natal I saw an immature *P. regulus* in company with a pair of Diamond Sparrows . . . the plantation was put under observation the following day, and the Honey Guide was found to be still in company with the Sparrows, and was shot, the specimen now being in the British Museum.
>
> *Petronia superciliaris* is general in East Africa wherever *Prodotiscus* occurs, and I myself feel . . . that it constitutes one of the foster-parents of the genus. The fact that *Prodotiscus regulus* was seen by Millar prying into holes . . . is in keeping with this possibility.

If the young *Prodotiscus* had been seen but once with the *Petronia* it could have been dismissed as a coincidence, but the fact that it remained with them for two days makes it difficult to look upon this record as other than a definite host-parasite combination. It is all the more surprising that this species should be found to parasitize a hole-nester, like the larger honey-guides of the genus *Indicator,* while its congener *P. insignis* lays its eggs in open cuplike nests of white-from eyes, warblers, and flycatchers.

Another observation of interest here, and corroborating the above in that it involves again a bird that nests in a hole (or what amounts to one), is the following inconclusive one kindly related to me by W. L. Chiazzari, who recorded it in the Richmond District, central Natal.

> Insofar as its breeding habits are concerned, it has been suggested that it might parasitize some of the flycatchers, and, while such species such as the paradise flycatcher (*Terpsiphone viridis*) and the Cape Batis (*Batis capensis*) breed in some numbers in these plantations, of the many nests I have examined of these and a variety of other birds, such as *Zosterops virens* who favor the wattles as nesting sites, I have not found any evidence to support this. However, it is the purpose of this letter to submit for what it is worth an incident that was recorded from this farm.
>
> On the morning of February 5, 1939, a female *Prodotiscus* (I judged this by the plumage which was more gray on the breast and throat) was seen to leave the globular-shaped mud nest of a pair of stripe-breasted swallows (*Hirundo cucullata*), who had constructed it against a beam and the ceiling of the verandah on the first floor. The nest however, had been usurped by a pair of swifts (*Apus caffer*) who had laid in it some days previously. The honey-guide, upon leaving the nest, perched on the balustrading enclosing the verandah, remained for a few minutes, and then departed to some nearby trees.
>
> In great excitement I examined the nest only to be disappointed when I found it only contained the two elongated white eggs of the swift. A watch was kept for the next few days in the hopes of seeing the honey-guide return, and, although it was observed on the railings, I did not see it enter the nest again. This may have happened during the hours I was not at my post!
>
> In order to set before you the complete picture and perhaps complicate matters, it is well to add to the above the fact that between the ceiling and the flooring of the verandah on the ground floor and the verandah in question a hive of bees had established themselves. The questions I now ask myself are these—was the honey-guide attracted there by the hive or did it come with the intention of parasitizing the swallow's nest? In that case the location of the hive may have been coincidental.
>
> I am inclined to favor the latter as being the import behind the appearance of the honey-guide on the verandah insofar as while I did not again observe the bird at the nest, it showed no interest whatsoever in the bees around, or the location of the hive. It may, of course, have been waiting for someone to open the hive before showing signs of interest. Combined with this was the fact that there were unavoidable comings and goings in and around the house which may have disturbed the bird and a further disturbing element in the present tenants of the nest whose arrivals and departures were always rapid and sudden!
>
> Unfortunately I was not able to complete my observations as I had to return to University. I was sorely tempted to collect the bird in question for examination but on second thought I decided it was worth while asking my father to keep it under further observation and to examine the nest once more. After one more appearance it failed to show up again.

Another less complete and conclusive observation indicative of the bird's interest in hole-nesters is the following one made at Fort Beaufort in the eastern Cape Province by J. Sneyd Taylor and relayed to me by C. J. Skead. A sharp-billed honey-guide was seen flying up to and looking into the holes in the bank of a donga occupied by pied starlings (*Spreo bicolor*) and horus swifts (*Micropus horus*). It entered several holes, disappearing into some for a second or two, before flying off.

Songs and Calls

On most of the 10 or 12 times that I have observed this bird it was silent, but on a few occasions I heard it give a low, guttural *tsip* or *tsep*, repeated two or three times; and a wounded bird gave a rather nasal rasping scream several times in rapid succession when I picked it up. Vincent (in A. Roberts, 1930b) describes the usual note he heard as a loud, rasping *zeet, zeet.* He also mentions that as the birds, restlessly flitting about in the trees, were on the point of alighting they uttered a subdued, but harsh, squeaking, stuttering chatter. Chiazzari (in litt.) renders the usual note in the same way as Vincent, *zeet.*

Late in winter (August 30) near Howick, Natal, I saw a *Prodotiscus regulus* fly up from a blackberry thicket where it had been associating with some waxbills (*Lagonosticta* and *Estrilda*) and perch about 15 feet up in a small dead tree. It immediately sat up very erectly, threw its head back, and began to sing, giving two notes *tseeeu tseeeu,* something like those of the Cape canary *Serinus canicollis.* As it sang it pumped its tail several times and showed the white outer rectrices. I shot it and found it was an immature female with completely white outer tail feathers. The ovary was only slightly enlarged. If this performance was a "song" and not merely "call notes," it follows that the female sings. The way in which the bird threw back its head when starting to utter its notes reminded me of the way male birds frequently do when singing; it was a great surprise to find, on dissection, that the bird was a female.

Food and Feeding Habits

Adult: A number of observations of the sharp-billed honey-guide's method of feeding are available. Millar, near Durban (cited by Stark and Sclater, 1903, p. 156) found it fed on small insects generally, and often remained on one tree for a considerable time, seeking its food. In the eastern Cape Province, Skead (in litt.) watched one feeding leisurely in an acacia thicket. The bird would sit on a branch, cocking its head first one way, then the other, looking for food, which, if seen, was then taken. If none was found, it would flit to another branch and repeat the action. It differed in its food-finding from the Cape white-eyes (*Zosterops capensis*) and the black tits (*Parus niger*) with which it was associated in that it did not peer among the leaves as did these two species, but merely looked about, first in one direction, then in another. In Nyasaland, the Bensons (1948, p. 392) saw one hawking for insects on the wing like a flycatcher. When actually capturing an insect it tended to hover with its tail widely spread. Colonel Stockley (in litt.) saw a couple (pair?) of these birds working the undersides of large acacia branches for insects in the bark. In their searching they reminded him of the spider hunters (*Arachnothera*) of southern Asia. This was on the Lorogi Plateau, Kenya Colony. Also in Kenya Colony, Williams writes me that he saw this species flying out from its perch, catching insects, and then returning to the same twig, like a flycatcher, thus agreeing with the observations of the Bensons. In the Thika area Williams has seen it in vicinity of native beehives, in company with other species of honey-guides, and suggests that it may be not uninterested in these hives, as in the stomach contents of most of the examples he collected there were quantities of beeswax, as in the species of *Indicator*, as well as insect fragments including lepidopterous and coleopterous larvae.

Butler (in Sclater and Mackworth-Praed, 1919, p. 640) found it feeding on the flowers of the tartar tree (*Sterculia cinerea*), where he repeatedly saw it. Stoehr (in Stoehr and Sclater, 1906, p. 106) found it flitting about, like a warbler or a flycatcher, among the bushes in Northern Rhodesia. Davies (1907, p. 193) saw several of this species hunting for insects among the branches of black wattle trees in Pondoland; Beven (1946, p. 67), in the Transvaal, watched two of them feeding on membracids like warblers. In the Chyulu Hills, Kenya Colony, van Someren (1939, p. 53) found this honey-guide feeding on scale insects. In the stomach of one that he shot was a mass of coccids which had been removed from a *Loranthus*.

Vincent (in A. Roberts, 1930b) saw one feeding avidly on the American blight or wooly aphis (*Schizoneura lanigera*) on apple trees in a neglected orchard. A few weeks later he saw three more, together with a pair of green white-eyes (*Zosterops virens*) and a black tit (*Parus niger*) in the same tree, again feeding on the wooly aphis.

All the individuals that I observed were either perching quietly, not feeding, or were found by seeing them fly out after passing insects, when their white outer tail feathers and undulating flight made them readily identifiable. The gizzards of seven specimens collected contained remains of unidentified small insects and a mass of whitish yellow waxy material that may have been either beeswax or the exudations of scale insects.

Aside from the one fledgling still attended by its foster parents, *Petronia superciliosus*, when collected by Vincent, we have no knowledge of the food the young honey-guide may get. In its stomach was a deep golden yellow sticky mass flecked with small insect remains (data from label of specimen in British Museum). What the sticky mass may have been is unknown, but the fact that the bird was still attended by its foster parents would seem to preclude the possibility of its being wax, as the yellow-throated sparrow does not normally eat wax in any quantity, as far as known.

Miscellaneous Behavior

The flight of this honey-guide is decidedly undulating, with somewhat irregular timing to the wing beats, which are not in rapid succession but a few beats followed by a short dipping glide. The tail is usually kept widely spread during flight, the white on the outer rectrices being a conspicuous field mark.

I have never seen this bird "mobbed" by other birds as some of the forms of *Indicator* are occasionally. However, Beven (1946, p. 67) saw one chased several times by a sunbird (*Chalcometra senegalensis*), and in Kenya Colony Williams saw one pursued by a pair of rock sparrows (*Petronia superciliaris*). The honey-guide erected its fluffy white flank feathers, which seemed to excite the sparrows.

The head bobbing mannerism of this bird is quite pronounced, and often helps the observer to distinguish it from *Alseonax* in the field. Skead (1951, p. 62) describes this bobbing as a "sort of circular rolling of the head, as though some constricting force around the neck were causing the bird to ease the discomfort by moving its head all the time." The Bensons (1948, p. 392) emphasize the fact that this bobbing is lateral, not vertical, and suggest that in *P. insignis* the motion is vertical rather than lateral.

Description

Adult (sexes alike in coloration): Forehead, lores, cheeks, auriculars, crown, occiput, nape, and entire upperparts of body and wings dark hair-brown to chaetura drab, the scapulars and upper wing-coverts edged and tipped (in fresh plumage) with pale hair-brown; the secondaries externally edged with pale hair-brown, internally with drab gray; two median pairs of rectrices dark hair-brown to chaetura drab, the outer ones white with very broad tips of dark hair-brown, these dark areas continuing about one-third to one-half way down the edges of the feathers; chin and throat pale to very pale smoke gray to almost white; breast, sides, and lower flanks light grayish drab to drab, palest medially; abdomen white, more or less washed with buffy grayish; under tail-coverts white; on the upper part of the flanks a patch of long silky white feathers; under wing-coverts and axillars white; iris dark grayish brown; bill very dark gray to almost black; tarsi and toes pale gray to dark blackish gray. Measurements in millimeters: male: wings 75–84; tail 48–56; culmen from base 10–13; tarsus 11–13; female: wings 75–83.5; tail 48–53.5; culmen from base 11.5–13; tarsus 11–12.

JUVENAL (sexes alike): Similar to the adult, but generally paler above; chin and throat averaging slightly duskier, abdomen less pure whitish; three lateral pairs of rectrices white without any brown tips, sometimes with a partial narrow edging of brown on the inner two of these three pairs; iris dark brown; bill blackish or sepia, orange at the gape; feet gray to blackish.

NATAL DOWN: Not known, if any.

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